

**FUNCTION OF SONG
IN CHIPPING SPARROWS**
(Spizella passerina)

by

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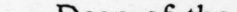
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I also attempted to determine song function by quantifying song output relative to reproductive status. High levels of singing were observed only in unmated males ($n=27$). Singing activity effectively ceased after pairing. This pattern of singing rejects the "dual function" hypothesis and supports an alternative that song has only a mate attraction function.

Information from a limited number of studies has been used to develop assumptions about the relationship of song function and complexity. These assumptions relate the function of mate attraction to song complexity, while territorial song is expected to be short,

simple, and stereotyped. How

ABSTRACT

The functions most commonly ascribed to bird song are mate attraction and territory defense. These are combined into the "dual function" hypothesis. I tested this hypothesis to determine if these are the functions of song in chipping sparrows (*Spizella passerina*).

I performed a series of neighbor/stranger song playbacks to test the territory defense portion of the "dual function" hypothesis. If song has a territorial function, songs of different individuals might be recognized by territory owners and might elicit different levels of response. However, territorial male chipping sparrows did not respond differently to neighbor and stranger song playbacks either early in the breeding cycle ($n=18$) or after the onset of incubation ($n=10$). There was also no decrease in the level of response between the early and late playbacks. These experiments did not elicit the pattern of results predicted on the basis that song has a territorial function.

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Information from a limited number of studies has been used to develop assumptions about the relationship of song function and complexity. These assumptions relate the function of mate attraction to song complexity, while territorial song is expected to be short,

simple, and stereotyped. However, chipping sparrow song appears to function solely in mate attraction, while its physical features resemble what could be considered typical territorial song. Possible relationships between the physical features and function of chipping sparrow song are discussed.

A variety of functions including maintenance of social organization (Hinde 1956), mate attraction (Catchpole 1973), attraction of females for extra-pair copulations (Møller 1988), synchronization of reproductive behaviors between mates (Brockway 1969; Hinde and Steel 1978; Morton *et al.* 1985), mate guarding (Mace 1987), and tutoring young as part of the song learning process (Greig-Smith 1982; Zann 1990). A functional interpretation of song is often difficult because one song may transmit multiple items of information (species, sex, identity, location). The "dual function" hypothesis dominates most explanations of why birds sing: a male sings both to attract females and to repel males. Tinbergen (1939) called this "advertising" song.

Studies of song function have involved muting males (Peck 1972; Smith 1976; McDonald 1989), removing territorial males and "occupying" their territories with broadcasts of their own songs (Krebs 1977; Krebs *et al.* 1978; Yasukawa 1981), playbacks of neighbor, stranger, and self songs to territorial males (Weeden and Falls 1959; Brooks and Falls 1975; Searcy *et al.* 1981; Weary *et al.* 1987), measuring song's ability to elicit copulation solicitation displays from hormone-primed females (Searcy and Marler 1981; Catchpole 1986), and interpreting song output in a seasonal context (Catchpole 1973; Slagsvold 1977; Greig-Smith 1982; Johnson and

INTRODUCTION

Bird song serves a variety of functions including maintenance of social organization (Hinde 1956), mate attraction (Catchpole 1973), attraction of females for extra-pair copulations (Møller 1988), synchronization of reproductive behaviors between mates (Brockway 1969; Hinde and Steel 1978; Morton *et al.* 1985), mate guarding (Mace 1987), and tutoring young as part of the song learning process (Greig-Smith 1982; Zann 1990). A functional interpretation of song is often difficult because one song may transmit multiple items of information (species, sex, identity, location). The "dual function" hypothesis dominates most explanations of why birds sing: a male sings both to attract females and to repel males. Tinbergen (1939) called this "advertising" song.

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Kermott, *in press*). Because song may contain one or more messages, the meaning of which may vary with the context of both the signaller and receiver, a combination of these techniques may be needed to determine the function of song.

I tested the "dual function" of song hypothesis in a population of chipping sparrows (*Spizella passerina*) by performing a series of neighbor/stranger song playbacks to territorial males. This type of experiment is designed to simulate territorial encounters with songs of familiar and unfamiliar conspecifics posing potentially different levels of threat and eliciting correspondingly different levels of response. As the breeding season progresses, the relative difference in the threat posed by familiar and unfamiliar songs also may change. If song has a territorial function, both the level of response and degree of difference in response to different playbacks are expected to change over the breeding season.

I also attempted to determine song function by quantifying song output relative to stage of reproduction. Comparing a male's song output before and after pairing, incubation, and desertion by his mate is useful in evaluating the "dual function" hypothesis. Decreased but persistent song production throughout the season, even after pairing, supports the hypothesis that song helps both in attracting a mate and in maintaining the territory through the rest of the breeding season. Cessation of song production after pairing is inconsistent with this hypothesis, and supports the alternative that song has solely a mate attraction function.

Playback Experiments

The ability of birds to discriminate among individuals by song can influence reproductive success by allowing for mate and parent/offspring recognition, and possibly for recognition of other members of the population. Discrimination among individuals by song has been demonstrated in birds by observations that territorial males respond more strongly to playbacks of strangers' songs than to those of neighbors' songs (Weeden and Fall 1959; Emlen 1971; Goldman 1973; Brooks and Falls 1975; Searcy *et al.* 1981). Such recognition is presumed advantageous in that it allows for reduction of aggression in maintaining territorial boundaries in situations where an intruder poses little threat to the resident's reproductive success (Marler 1960).

Marler and Isaac (1960) proposed that advertising song is subject to conflicting selective forces by the necessity for species and individual recognition. Species recognition, which is especially important in intersexual communication, is best encoded in features that are consistent in all members of the species or population. Individual recognition and neighbor/stranger discrimination require features that are highly stereotyped within an individual but vary noticeably among individuals. The learning mechanism involved in neighbor/stranger discrimination appears to be classical habituation: response to neighbor song declines over the season (Falls 1982; Ydenberg *et al.* 1988). A single song repeated over and over lends itself to habituation, and neighbor/stranger discrimination has been demonstrated most clearly in species that have only one song type.

The idea linking familiarity to reduced aggression is widespread in the literature on bird song and its evolution. A song type and singing behavior that contribute to the efficient allocation of energy in territory maintenance through neighbor recognition can be argued to have an intra-sexual selective advantage (Weeden and Falls 1959).

Although song may contain sufficient inter-individual variation to allow for individual recognition, and is delivered in a manner conducive to habituation, neighbor/stranger discrimination may not always be elicited by song playbacks. Resident males are most likely to direct aggression toward individuals that represent a threat. Certain experimental conditions, such as the timing of the playback relative to the subject's reproductive status, may reduce the difference in neighbor/stranger threat value. A resident male whose mate is building a nest or laying eggs might not show a difference in his response to neighbor and stranger song playbacks because all conspecific males represent a threat to his paternity in the form of extra-pair copulations. Later in the breeding cycle, when the female is no longer sexually receptive, stranger playbacks may elicit a stronger response because strangers may pose a greater threat to a resident male than do his established neighbors since established males have been observed to lose part of their territories to newly arrived males.

I performed a series of neighbor/stranger song playback experiments to resident male chipping sparrows. Playbacks were performed both when a male's mate was building or laying and again when she was incubating to examine the influence of familiarity and

reproductive status on a male's response to song playbacks (Figure 1).

Breeding Season Singing Patterns

In many species, there is an association between seasonal breeding activities and song output. However, relatively few studies have quantified the relationship between song output and events in birds' breeding cycles (Catchpole 1973; Slagsvold 1977; Greig-Smith 1982; Cuthill and Hindmarsh 1985; Møller 1988; Johnson and Kermott, *in press*). Output is generally greatest just after the start of the breeding season and decreases over the course of the season. Although this decrease may be significant, some singing persists throughout most of the season. The early peak in production is usually associated with a male's attempt to attract a mate (intersexual communication), while persistent song over the rest of the season is presumed necessary to maintain a territory (intrasexual communication). In this case, the dual functions assumed in Tinbergen's (1939) "advertising" song seem likely. Studies of species with two songs have demonstrated that certain songs, such as the "A" song of the black-throated green warbler (*Dendroica virens*) and the "unaccented ending" song of the chestnut-sided warbler (*Dendroica pennsylvanica*), are used primarily in the context of intrasexual interactions, while the "B" and "accented ending" songs are sung during intersexual interactions (Smith 1959; Morse 1970; Lein 1972; Lein 1978; Kroodsma 1981).

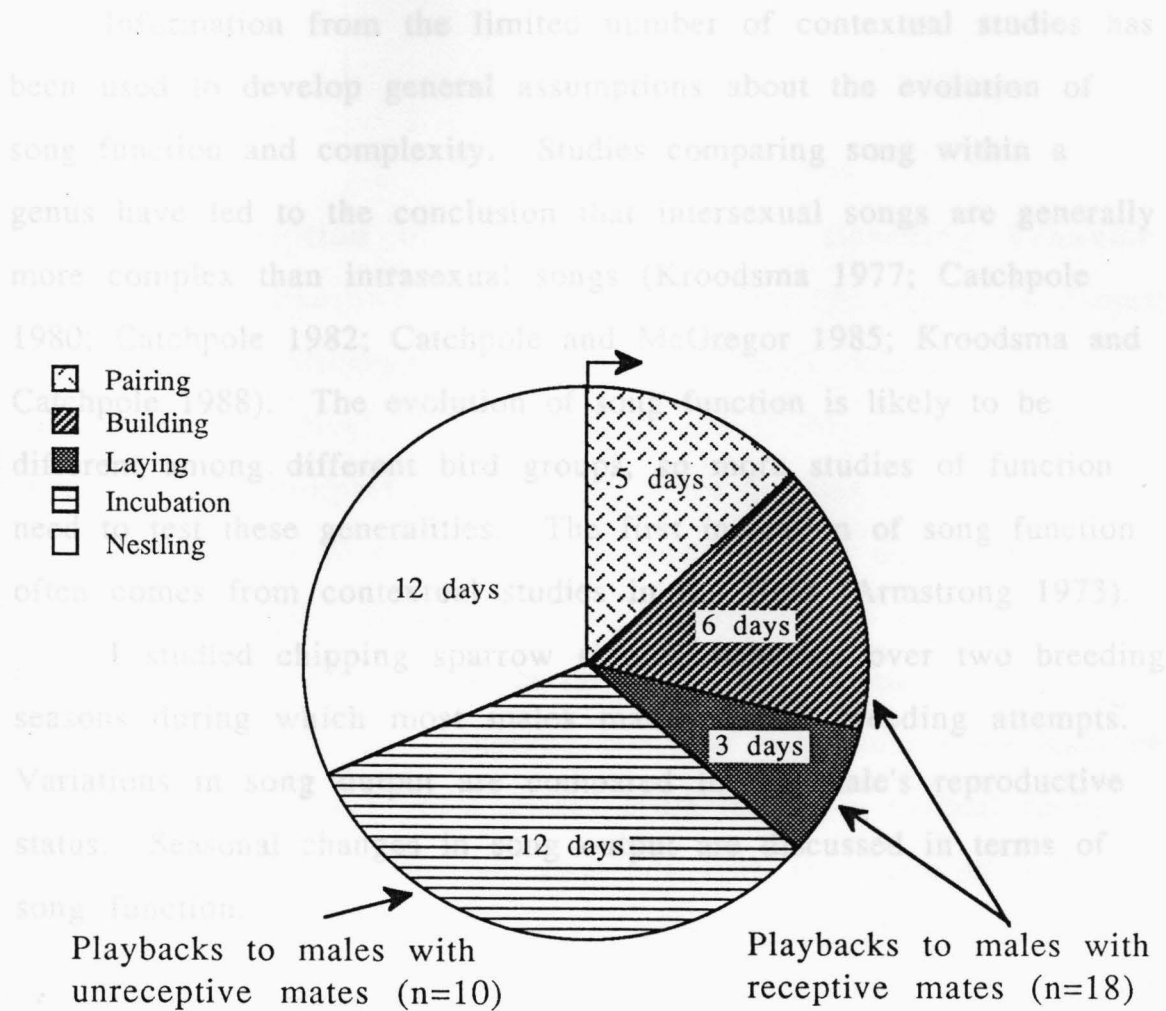


Figure 1. Timing of playbacks relative to breeding cycle (38 days total)

Information from the limited number of contextual studies has been used to develop general assumptions about the evolution of song function and complexity. Studies comparing song within a genus have led to the conclusion that intersexual songs are generally more complex than intrasexual songs (Kroodsma 1977; Catchpole 1980; Catchpole 1982; Catchpole and McGregor 1985; Kroodsma and Catchpole 1988). The evolution of song function is likely to be different among different bird groups, so more studies of function need to test these generalities. The first indication of song function often comes from contextual studies in the field (Armstrong 1973).

I studied chipping sparrow singing behavior over two breeding seasons during which most males made several breeding attempts. Variations in song output are compared to the male's reproductive status. Seasonal changes in song output are discussed in terms of song function.

Early in the season, nest building typically begins within five days of pair formation; in mid-June and early July, it often commences within a day of pair formation. The female does all the building, but she is accompanied constantly by her mate. During these early stages of the reproductive cycle, copulations were observed all through the morning (236 copulations in 5245 minutes of observation) (Figure 2). Nest building can last 3-6 days and is immediately followed by egg laying. During this stage, copulations

METHODS

General Description of Chipping Sparrow Breeding Behavior

Chipping sparrows breed from early May through early August in northwestern Minnesota. Males were already defending areas at the time of my arrival on 10 May 1989 and 11 May 1990. Since this species is monomorphic, the arrival date of females is not known, but the first activities of pair formation were observed on 17 May 1989 and 14 May 1990. Females entering a territory are chased initially by the resident male. Male-female chases are circular, contained within the territory, and generally conclude with both individuals on the ground, while male-male chases often include a vertical flight in which individuals grapple, and conclude with the pursuing male stopping or turning back at a certain point (Keller 1979). Male-female chasing eventually decreases and the pair begins to move together around the territory.

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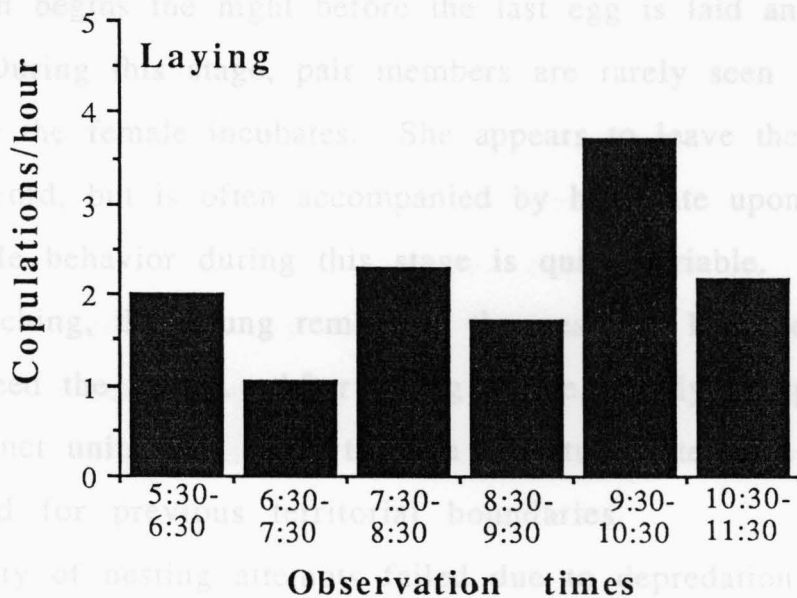
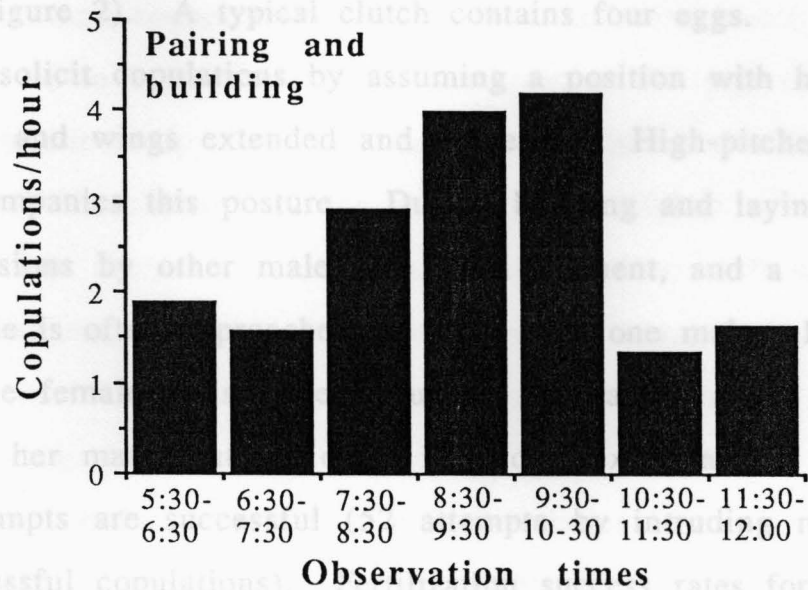


Figure 2. Frequency of copulations relative to reproductive stage

were also observed frequently (56 copulations in 1615 minutes of observation) (Figure 2). A typical clutch contains four eggs.

Females solicit copulations by assuming a position with head and tail raised and wings extended and quivering. High-pitched squeaking accompanies this posture. During building and laying, territorial intrusions by other males are most frequent, and a soliciting female is often approached by more than one male. In some cases, the female resists the intruders' approaches and copulates with her mate, but, in other instances, extra-pair copulation attempts are successful (52 attempts by intruding males with two successful copulations). Fertilization success rates for extra-pair copulations are unknown.

Incubation begins the night before the last egg is laid and lasts 10-12 days. During this stage, pair members are rarely seen together. Only the female incubates. She appears to leave the nest of her own accord, but is often accompanied by her mate upon returning. Male behavior during this stage is quite variable.

After hatching, the young remain in the nest for 10-12 days. Both parents feed the young. After young fledge, family groups remain as distinct units, but move through the study site with no apparent regard for previous territorial boundaries.

A majority of nesting attempts failed due to depredation of eggs or young (46 nesting attempts were made by 28 males, and eight of these attempts were successful). The major sources of nest failure were believed to be red squirrels (*Tamiasciurus hudsonicus*), common crows (*Corvus brachyrhynchos*), and blue jays (*Cyanocitta*

cristata) (Keller 1979). Following nest destruction, some pairs are remained together and began nest building in a different location in the original tree or in a new tree in the territory, or the pair moved to a new area in the study site. In other cases, females abandoned their mates which then advertised for new females. When a nest was built in a new tree, territorial boundaries tended to shift with the new nest tree near the center of the defended area.

Chipping sparrows generally maintain monogamous relationships during the breeding season, but previous studies suggest that some variation exists in mating relationships. Walkinshaw (1959) observed a single nest containing eight eggs that was apparently attended by two females mated to the same male. Keller (1979) reported one case of polygyny in 32 pairings over two seasons, and I observed two cases of polygyny in 46 pairings over two seasons. I also observed two extra-pair copulations. Middleton and Prescott (1989) monitored nine pairs and observed five cases of monogamy, two cases of polygyny, extra-pair copulations on two territories, and helpers-at-the-nest on one territory. It appears that chipping sparrow breeding behavior is variable, and males might sometimes pursue an opportunistic strategy to obtain or enhance reproductive success (Middleton and Prescott 1989).

Description of Study Site

This study was conducted at the University of Minnesota Forestry and Biological Station, located in Itasca State Park in

northwestern Minnesota. The park contains a variety of mature

coniferous and deciduous forests. However, chipping sparrows are found primarily in open areas with short grass, especially near park buildings.

The Forestry and Biological Station is bordered by Lake Itasca to the west, by forest to the north and east, and by bog to the south. The grounds of the station have a flat topography and consist of a mixture of mowed lawns and woods around the buildings. There are two large open areas (Figure 3). The most common tree is white spruce (*Picea glauca*). Also present are white pine (*Pinus strobilus*), red pine (*Pinus resinosa*), tamarack (*Larix laricina*), and basswood (*Tilia americana*). Most canopy trees are 15-30 m tall.

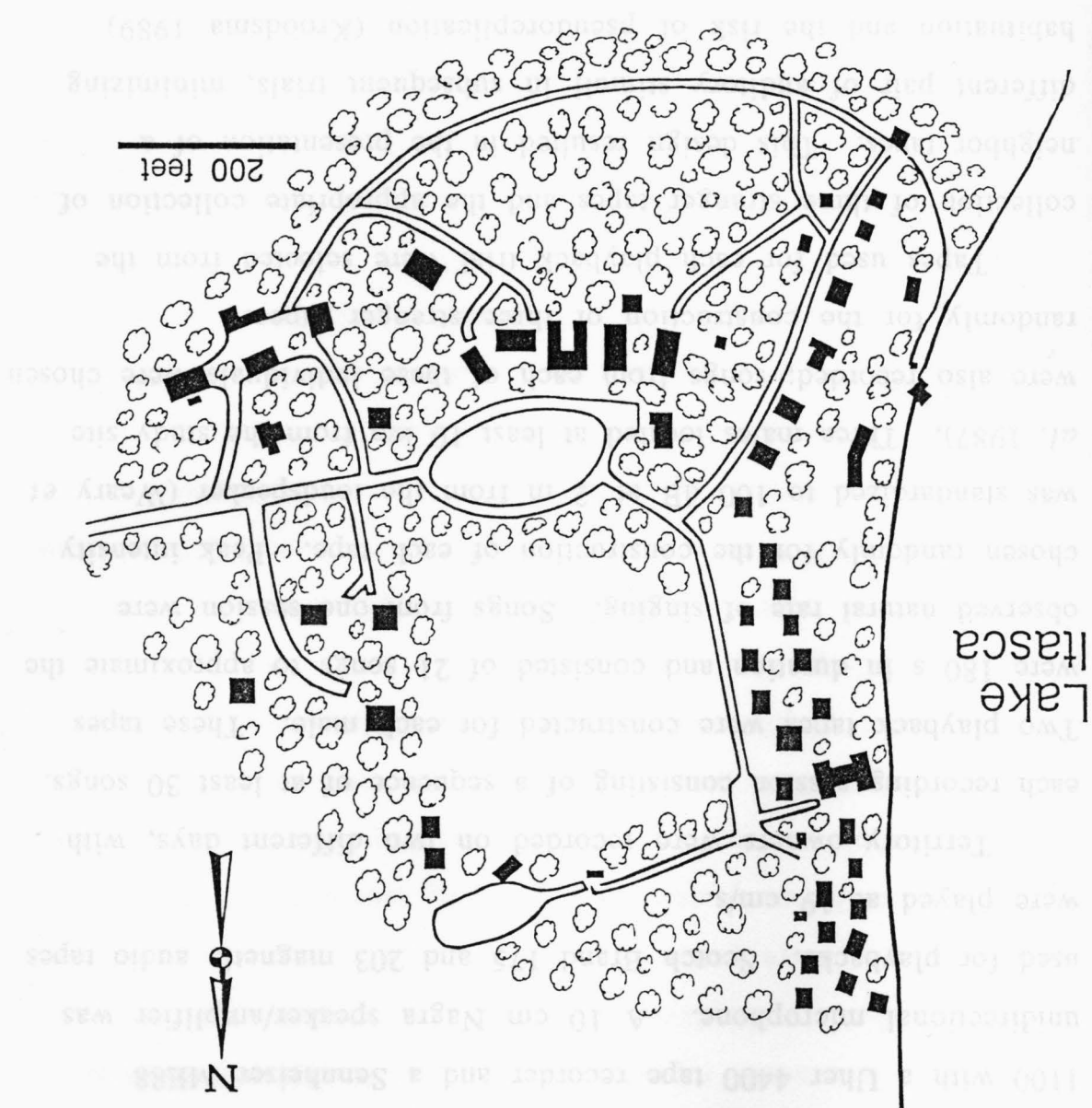
Unlike the study sites of Walkinshaw (1944 and 1959), trees at Lake Itasca are quite tall. Much of the "common knowledge" of chipping sparrow breeding behavior, such as the typical height of nests, has come from observations made in suburban areas and college campuses where trees were shorter. In my study area, nest heights ranged from 1-24 m, with a mean value of 11 m.

Banding

Nine of 12 males in 1989 and 10 of 16 males in 1990 were banded with an aluminum band from the U.S. Fish and Wildlife Service and a unique combination of three colored leg bands. Most birds were captured early in the season in mist nets placed along edges of open areas. Playbacks were not used in capturing birds.

observations between 0530 and 1300. Behavior of a focal male was
 Reproductive status of territorial males was monitored by daily

Figure 3. Map of study site



Playback Experiments

Experimental Tapes

Males singing on territory were recorded between 0700 and 1100 with a Uher 4400 tape recorder and a Sennheiser ME88 unidirectional microphone. A 10 cm Nagra speaker/amplifier was used for playbacks. Scotch Brand 175 and 203 magnetic audio tapes were played at 19 cm/s.

Territory owners were recorded on two different days, with each recording session consisting of a sequence of at least 30 songs. Two playback tapes were constructed for each male. These tapes were 180 s in duration and consisted of 21 songs to approximate the observed natural rate of singing. Songs from one session were chosen randomly for the construction of each tape. Peak intensity was standardized to 100 dB at .2 m from the loudspeaker (Weary *et al.* 1987). Three males located at least 10 km from the study site were also recorded; songs from each of these individuals were chosen randomly for the construction of three stranger tapes.

Tapes used for each playback trial were selected from the collection of three stranger tapes and the appropriate collection of neighbor tapes. This design resulted in the presentation of a different pair of auditory stimuli in subsequent trials, minimizing habituation and the risk of pseudoreplication (Kroodsma 1989).

Design and Procedures

Reproductive status of territorial males was monitored by daily observations between 0530 and 1200. Behavior of a focal male was

sampled continuously during 20 minute observation sessions (Martin and Bateson 1986). Individuals were observed in a random order each morning. Because it was not possible to visually inspect the contents of most nests, reproductive status of a pair was inferred from the behaviors displayed.

Playbacks were performed when a male's mate was building the nest or in the early days of egg laying (sexually receptive) and again after she had begun incubation (sexually unreceptive). Males were exposed to both neighbor and stranger songs during each trial, with the order of presentation randomized. The neighbor and stranger recordings that comprised one playback trial were separated by at least 30 minutes to reduce habituation.

During each trial, the loudspeaker was positioned 2-3 m above the ground in a tree along the boundary between the subject and the neighbor whose song was used. The speaker was directed toward the center of the subject's territory. Boundaries were identified during daily observations by the locations of the following behaviors (Keller 1979):

- 1) chases which ended with the individuals grappling in a vertical flight;
- 2) chases in which the pursuing individual stopped or turned back at a particular point; and
- 3) song.

The observer was located at least 20 m away and was in position to view both the subject's nest and the loudspeaker. The subject's behavior was observed for three periods: three minutes of

silence before the tape started, three minutes during the playback, and three minutes after the playback. The initial three minutes of silence during a playback served as a control because the birds were exposed to the presence of the loudspeaker and the observer, but not to song. Trials were initiated without reference to the activity of the subject.

Response variables

A subject's response was measured by the number of vocalizations and flights, the nearness of approach to the speaker, and the latency of response.

1. *Singing and Flying* -- Because levels of singing and flying vary daily, response measures of these behaviors during and after a playback were considered relative to the same measures before the playback (Searcy *et al.* 1981). An index of increase in singing and flying activity in response to a playback was calculated by dividing the sum of these activities during and after playback by the frequencies of these activities before playback. To avoid dividing by zero, 1 was added to the frequency of these activities in each period:

Wilcoxon matched-pairs signed-rank test (Catchpole 1977), the Mann-Whitney U test (Searcy *et al.* 1981), or one-way ANOVA (Weary *et al.* 1981). Each univariate test is expected to produce rejection of the null hypothesis 5% of the time at $\alpha = .05$ when the null hypothesis is in fact true (Type I error), the probability of producing significant results when only (flights before +1) has actually occurred

$$\text{Song increase} = \frac{(\text{songs during} + 1) + (\text{songs after} + 1)}{(\text{songs before} + 1)}$$

$$\text{Flight increase} = \frac{(\text{flights during} + 1) + (\text{flights after} + 1)}{(\text{flights before} + 1)}$$

In some cases, the subject was not seen during the initial three minutes of silence; under these circumstances, no index of flight increase could be determined.

2. *Approach* - Nearness of approach was recorded as the distance (m) between the speaker and the closest approach during the playback.

3. *Latency* - Latency was recorded as the time (s) between the beginning of the playback tape and the first observed change in behavior such as singing, calling, or flying.

Greater magnitudes of increase in singing and flying activity correspond to a stronger response, while smaller magnitudes in approach to the speaker and latency correspond to a stronger response.

Analysis

Similar data from previous playback experiments have been subjected to a series of univariate significance tests such as the Wilcoxon matched-pairs signed-rank test (Catchpole 1977), the Mann-Whitney U-test (Grove 1981), the t-test (Searcy *et al.* 1981), or one-way ANOVA (Weary *et al.* 1987). Since each univariate test is expected to produce rejection of the null hypothesis 5% of the time at $\alpha = .05$ when the null hypothesis is in fact true (Type I error), the probability of having at least one of the tests in a series produce significant results when only chance variation has actually occurred

increases as the number of tests increases (Harris 1975). Because the variables used to measure response in playback experiments are not independent, a series of univariate significance tests is not a powerful method for testing hypotheses about the response of subjects to different types of playbacks.

Multivariate techniques have been developed for dealing with the simultaneous variation of two or more variables while controlling for experiment-wise error rate (Sokal and Rohlf 1981; Harris 1975). Multivariate techniques combine the original variables, and tests of significance are based on the distribution of the combined variable (Harris 1975).

Here, multivariate analysis of variance (MANOVA) is used to assess the effect of the type of playback (neighbor vs. stranger), the breeding status of the subject (males with receptive mates vs. males with unreceptive mates), and the year of the study (1989 vs. 1990) on the response of the subjects. This analysis is used to test for the possibility of neighbor/stranger discrimination and was performed on data collected from males with sexually receptive mates and on data collected from males with sexually unreceptive mates. The same analysis is used to compare the overall level of response of males at different reproductive stages. A possible year effect is tested for because differences in the number of breeding males on the study site were observed in the two years of the study.

The same method of analysis is used to compare the response of males to the first and second playback in a trial. This is done to test for the presence of an effect of order on the subjects'

response. Presentation order was randomized, but sample size was small, so the potential effect of this condition needs to be examined.

Breeding Season Singing Patterns

Observation Sessions

Singing behavior of focal males was quantified by continuous sampling during 20 minute observation sessions. Individuals were observed in a random order between 0530 and 1200 daily. Notes on the immediate context, such as with whom the male was interacting and from where he was singing, were recorded. These observation sessions were also used to collect data on reproductive status and the location of territorial boundaries for the playback experiments.

Analysis

Hourly singing rates were determined from each male's daily song output. These rates were then used to determine average singing rates relative to three stages of the reproductive cycle: before pairing, while paired to sexually receptive females, and paired to females that were no longer sexually receptive.

A one-tailed Wilcoxon matched-pairs signed-rank test is used to test for differences in singing output by unpaired males and by males paired to sexually receptive females (Siegel 1956). A significant decrease in singing after pairing has been interpreted as evidence that the function of the song is primarily intersexual communication (Catchpole 1973).

A stronger test of the mate attraction hypothesis would be to experimentally remove the female of a pair and to observe effects on the singing behavior of the male (Krebs *et al.* 1981; Cuthill and Hindmarsh 1985). In this study population, many nesting attempts ended when the females abandoned their mates, and this provided a natural experiment analogous to female removals (Johnson 1983). I compared singing rates of males after they had been deserted to their singing rates during the reproductive stage preceding desertion. To test for a significant difference in singing activity I again used a one-tailed Wilcoxon matched-pairs signed-rank test.

Keller (1979) observed increased song production after a male's mate had begun incubation. Such an increase has also been observed in house wrens (*Aedon troglodytes*) (Johnson and Kermott, *in press*), song sparrows (*Melospiza melodia*) (Nice 1943) and snow buntings (*Plectrophenax nivalis*) (Tinbergen 1939), and has been interpreted as part of the male's attempts to attract additional mates. I used a one-tailed Wilcoxon matched-pairs signed-rank test to compare song production of males before and after the onset of incubation.

Description of inter- and intra-individual song variation

Songs used in constructing playback tapes represent a random sample of songs from an individual. Fifteen of these tapes were constructed for use in playback experiments and songs from these tapes were analyzed to describe the extent of inter- and intra-individual song variation. Temporal, frequency, and amplitude

parameters were measured in five songs from each individual. All measurements were made from sound spectrographs produced on a Unigon Uniscan II set with a spectral gain of 200, a frequency range of 0-10,000 Hz, and an average of 256 spectral counts. Tracings of spectrographs produced on a Kay 7029A Sona-graph with a wide band setting are included for visual inspection (Appendix I).

Song characteristics measured

I used the calipers on the screen of the Unigon Uniscan II to measure song duration, syllable length, inter-syllable interval, minimum frequency in the song, and frequency at the point in the syllable with the highest amplitude (dominant frequency). I also recorded whether the syllables in an individual's song first decreased and then increased in frequency (pattern 1), or *vice versa* (pattern 2) (Appendix I).

Analysis

A multivariate analysis of variance (MANOVA) was used to compare variation within five songs from an individual to variation among the songs of 15 individuals. This comparison is done to determine the potential for recognition of individuals by song.

RESULTS

Playback Experiments

Experiment One: Playbacks to Males With Receptive Mates

Seven trials were performed in 1989 and 11 in 1990. Resident males did not differ in response to neighbor vs. stranger song playbacks (Wilk's lambda= .9604, $F = .2613$, $df = 4,21$, $P = .9264$) (Table 1, Figure 4).

Experiment Two: Playbacks to Males With Unreceptive Mates

A second series of experiments was performed to resident males whose mates were no longer sexually receptive. Because of high levels of nest destruction, only four trials were performed in 1989 and six in 1990. Subjects in this experiment also showed no difference in their behavioral response to neighbor vs. stranger song playbacks (Wilk's lambda= .8337, $F = .3988$, $df = 4,8$, $P = .8045$) (Table 2, Figure 5).

Table 1. Response of males with receptive mates to neighbor vs. stranger playbacks

	<u>Songs</u>	/	<u>Flights</u>	/	<u>Approach</u>	/	<u>Latency</u>
Neighbor	3.8± .51 n=18		3.8± .50 n=12		6.1± 1.16 n=18		38.9± 12.47 n=18
Stranger	3.6± .81 n=18		3.8± .53 n=15		4.2± 1.07 n=18		28.2± 9.58 n=18

Wilk's lambda= .9604, $F = .2163$, $df = 4, 21$, $P = .9264$

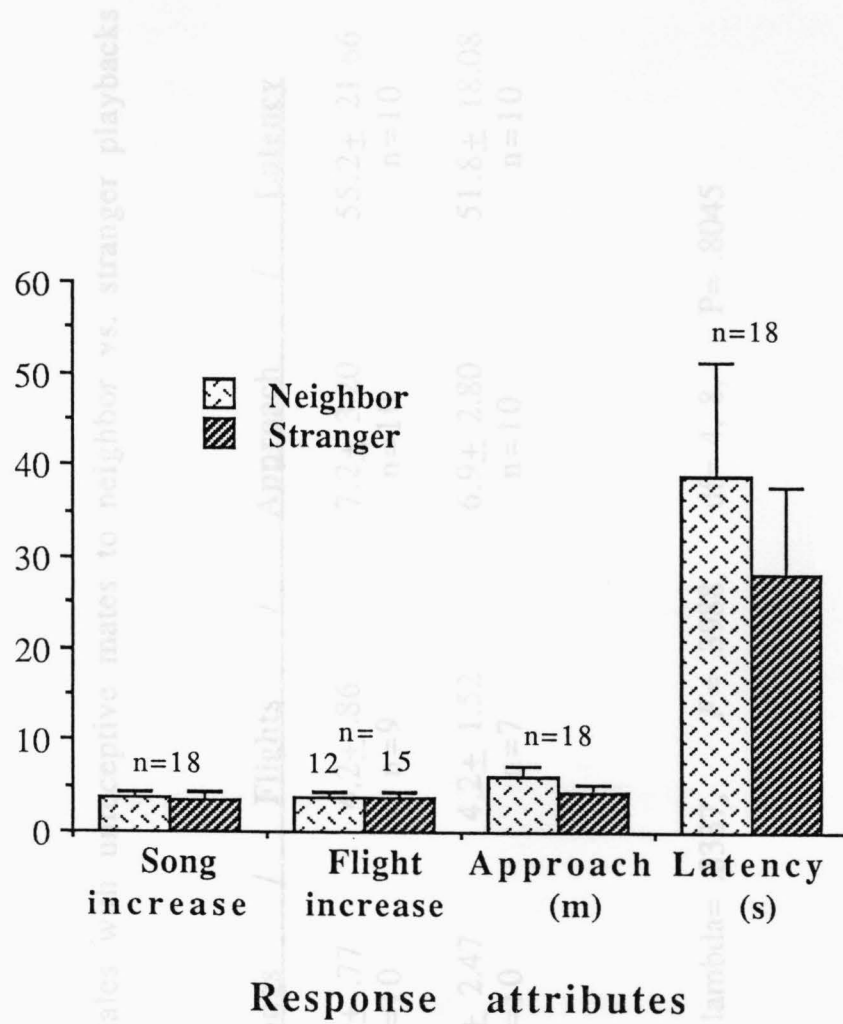


Figure 4. Mean response values of males with receptive mates

Table 2. Response of males with unreceptive mates to neighbor vs. stranger playbacks

	<u>Songs</u>	/	<u>Flights</u>	/	<u>Approach</u>	/	<u>Latency</u>
Neighbor	3.6± .77 n=10		4.2± .86 n=9		7.2± 3.20 n=10		55.2± 21.66 n=10
Stranger	5.4± 2.47 n=10		4.2± 1.52 n=7		6.9± 2.80 n=10		51.8± 18.08 n=10

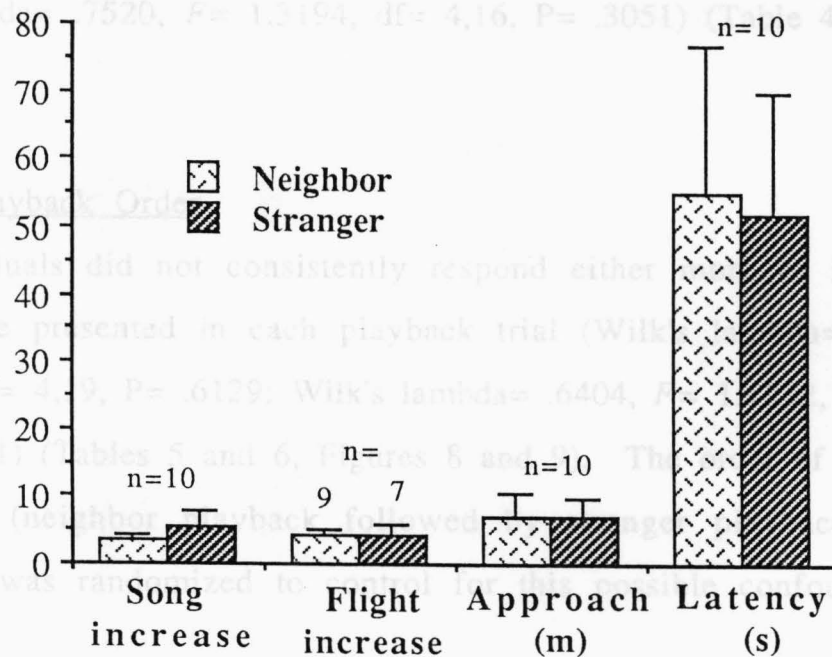
Wilk's lambda= .8337, $F = .3988$, $df = 4, 8$, $P = .8045$

Effect of Breeding Status

The breeding status of the subjects does not seem to affect their response. Strength of response to playbacks of neighbor song did not change with the subjects' reproductive status (Wilk's $\lambda = .9337$, $F = .2484$, $df = 4, 14$, $P = .9508$) (Table 3, Figure 6). The same was observed in subjects' response to stranger song playbacks (Wilk's $\lambda = .7520$, $F = 1.3194$, $df = 4, 16$, $P = .3051$) (Table 4, Figure 7).

Effect of Playback Order

Individuals did not consistently respond either more or less to the first tape presented in each playback trial (Wilk's $\lambda = .8744$, $F = .6821$, $df = 4, 9$, $P = .6129$; Wilk's $\lambda = .6404$, $F = 1.48$, $df = 4, 8$, $P = .4101$) (Tables 5 and 6, Figures 8 and 9). The order of presentation (neighbor playback followed by stranger playback, or vice versa) was randomized to control for possible order or handling effect.



Response attributes

Song Analysis

Figure 5. Mean response values of males with unreceptive mates

Songs of an individual are rather stereotyped, with no variation present in syllable length, syllable interval, and little variation in the minimum frequency of the song and the frequency of the point in the syllable with the greatest amplitude (Table 7).

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Song Analysis

Intra-individual Variation

Songs of an individual are rather stereotyped, with no variation present in syllable length, syllable interval, and little variation in the minimum frequency of the song and the frequency of the point in the syllable with the greatest amplitude (Table 7).

Table 3. Effect of breeding status: response to neighbor playbacks of males with receptive mates vs. males with unreceptive mates

	<u>Songs</u>	/	<u>Flights</u>	/	<u>Approach</u>	/	<u>Latency</u>
Receptive	3.8± .51 n=18		3.8± .50 n=12		6.1± 1.16 n=18		40.6± 12.47 n=18
Unreceptive	3.5± .77 n=10		4.2± .86 n=9		7.2± 3.20 n=10		55.2± 21.66 n=10

Wilk's lambda= .9337, $F = .2484$, $df = 4, 14$, $P = .9058$

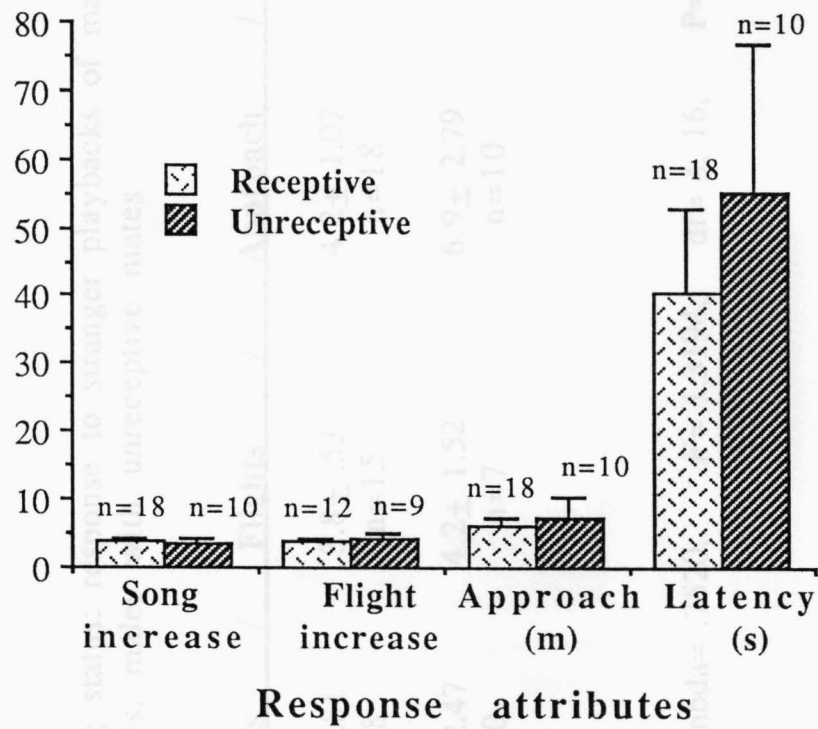


Figure 6. Response to neighbor playbacks of males with receptive mates vs. males with unreceptive mates

Table 4. Effect of breeding status: response to stranger playbacks of males with receptive mates vs. males with unreceptive mates

	<u>Songs</u>	/	<u>Flights</u>	/	<u>Approach</u>	/	<u>Latency</u>
Receptive	3.6± .81 n=18		3.8± .53 n=15		4.2± 1.07 n=18		28.2± 9.58 n=18
Unreceptive	5.4± 2.47 n=10		4.2± 1.52 n=7		6.9± 2.79 n=10		51.8± 18.08 n=10

Wilk's lambda= .7520, $F = 1.3194$, $df = 4, 16$, $P = .3051$

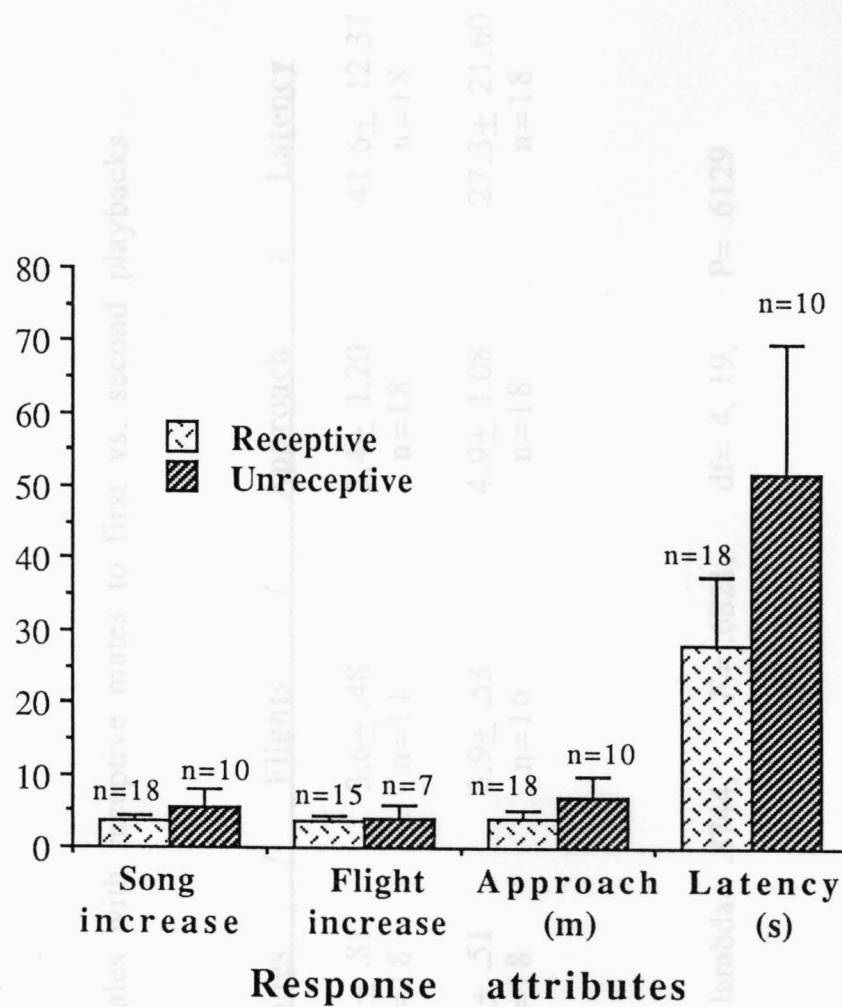


Figure 7. Response to stranger playbacks of males with receptive mates vs. males with unreceptive mates

Table 5. Response of males with receptive mates to first vs. second playbacks

	<u>Songs</u>	/	<u>Flights</u>	/	<u>Approach</u>	/	<u>Latency</u>
First playback	3.8± .81 n=18		3.6± .48 n=11		5.4± 1.20 n=18		41.6± 12.37 n=18
Second playback	3.5± .51 n=18		3.9± .53 n=16		4.9± 1.08 n=18		27.3± 21.60 n=18

Wilk's lambda= .8744, $F = .6821$, $df = 4, 19$, $P = .6129$

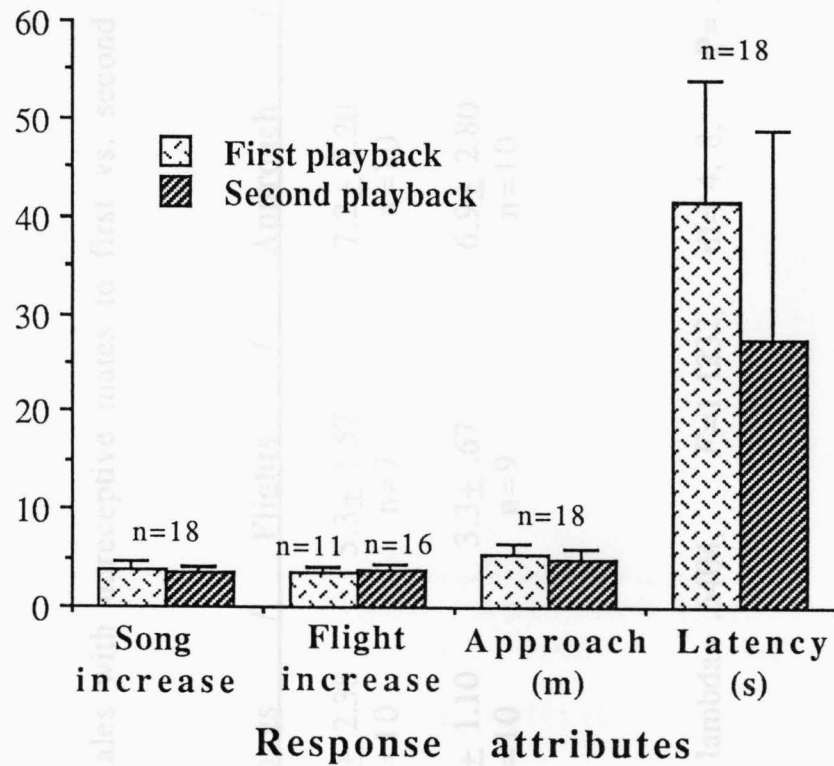


Figure 8. Response of males with receptive mates to first playbacks vs. second playbacks

Table 6. Response of males with unreceptive mates to first vs. second playbacks

	<u>Songs</u>	/	<u>Flights</u>	/	<u>Approach</u>	/	<u>Latency</u>
First playback	4.6 \pm 2.38 n=10		5.3 \pm 1.57 n=7		7.2 \pm 3.20 n=10		55.0 \pm 21.60 n=10
Second playback	4.3 \pm 1.10 n=10		3.3 \pm .67 n=9		6.9 \pm 2.80 n=10		52.0 \pm 18.17 n=10

Wilk's lambda= .6404, $F=1.1232$, $df= 4, 8$, $P= .4101$

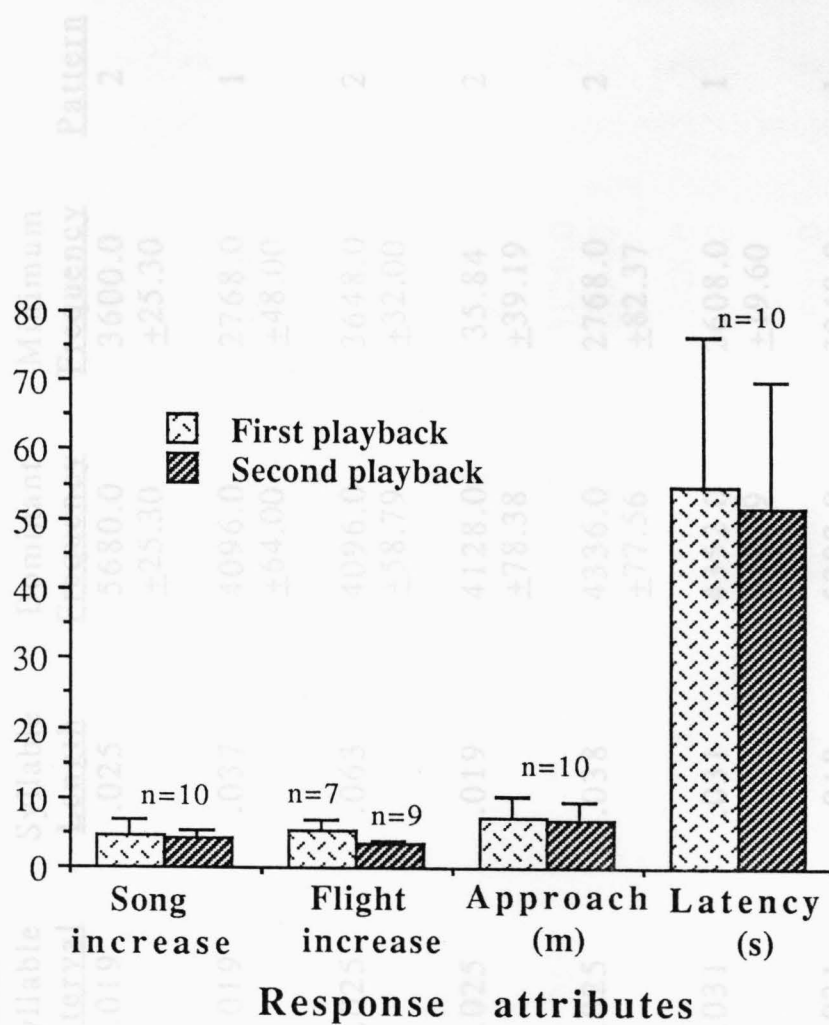


Figure 9. Response of males with unreceptive mates to first playbacks vs. second playbacks

Table 7. Means and standard errors of song measurements from 15 chipping sparrows, five songs per individual (some variables have standard errors of zero). Temporal characteristics measured in seconds and frequency characteristics in Hz.

<u>Individual</u>	<u>Song Length</u>	<u>Inter-syllable Interval</u>	<u>Syllable Length</u>	<u>Dominant Frequency</u>	<u>Minimum Frequency</u>	<u>Pattern</u>
1	2.4024 ±.33929	.019	.025	5680.0 ±25.30	3600.0 ±25.30	2
2	3.2368 ±.60539	.019	.037	4096.0 ±64.00	2768.0 ±48.00	1
3	2.3400 ±.19390	.025	.063	4096.0 ±58.79	3648.0 ±32.00	2
4	1.8832 ±.23424	.025	.019	4128.0 ±78.38	35.84 ±39.19	2
5	2.2554 ±.22920	.025	.038	4336.0 ±77.56	2768.0 ±82.37	2
6	2.3908 ±.14346	.031	.031	4352.0 ±40.79	2608.0 ±19.60	1
7	1.6954 ±.20765	.031	.018	5392.0 ±19.60	3248.0 ±74.19	1

<u>Individual</u>	<u>Song Length</u>	<u>syllable Interval</u>	<u>Inter-Syllable Length</u>	<u>Dominant Frequency</u>	<u>Minimum Frequency</u>	<u>Pattern</u>
8	2.0708 ±.18765	.031	.031	3840.0 ±35.78	2928.0 ±40.79	2
9	2.7016 ±.26678	.019	.025	4112.0 ±19.60	3568.0 ±19.60	2
10	1.8928 ±.23719	.025	.031	5184.0 ±39.19	4016.0 ±39.19	1
11	2.0748 ±.29140	.031	.025	5968.0 ±54.26	3184.0 ±77.57	2
12	2.1392 ±.26230	.025	.031	4864.0 ±29.93	4016.0 ±39.19	2
Stranger 1	2.3850 ±.06450	.031	.044	5296.0 ±16.00	3120.0 ±25.30	2
Stranger 2	2.6082 ±.10778	.031	.038	3888.0 ±19.60	3328.0 ±19.60	2
Stranger 3	2.1942 ±.07987	.025	.044	5360.0 ±43.82	3056.0 ±16.00	2

Inter-individual Variation

Inter-individual variation existed in each song feature quantified in the sample. Some features (syllable length, inter-syllable interval, and syllable pattern) that were consistent within individuals were also shared between two or more individuals (Table 7). However, MANOVA reveals that the combination of song features within any one individual is unique among the fifteen individuals included in the sample (Pillai's trace= 4.2297, $F = 23.5326$, $df = 70, 300$, $P < .0001$) (Table 7).

The most direct way to assess the potential for individual recognition is to determine the extent to which individuals in a population can be identified accurately by their songs. Different individuals can be distinguished by examining the sound spectrographs in Appendix I.

Breeding Season Singing Pattern

Unpaired males vs. Males with sexually receptive mates

Males showed a large decrease in song production after pairing in both years of the study ($P < .001$ in 1989, $P < .0001$ in 1990; Figures 10 and 11). There was no significant increase in singing activity by these males after their mates had begun incubation ($P > .05$ in 1989 and 1990; Figures 12 and 13). High levels of song production were demonstrated only by unmated males.

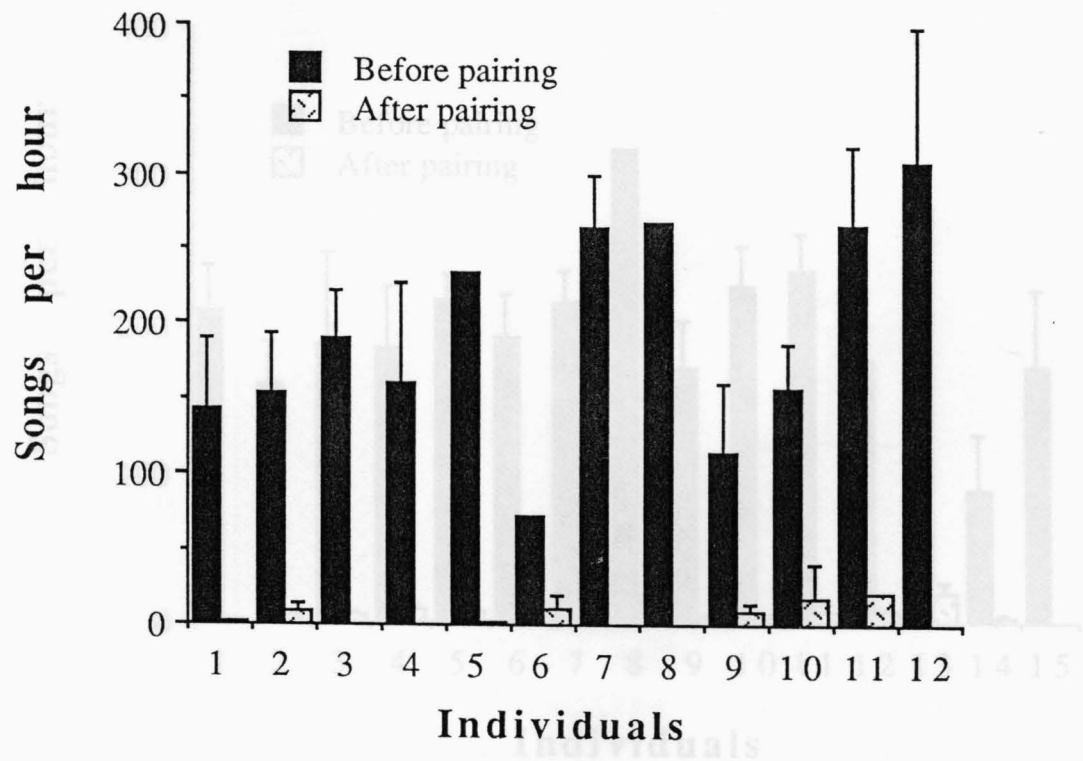


Figure 10. Song production by males before and after pairing- 1989

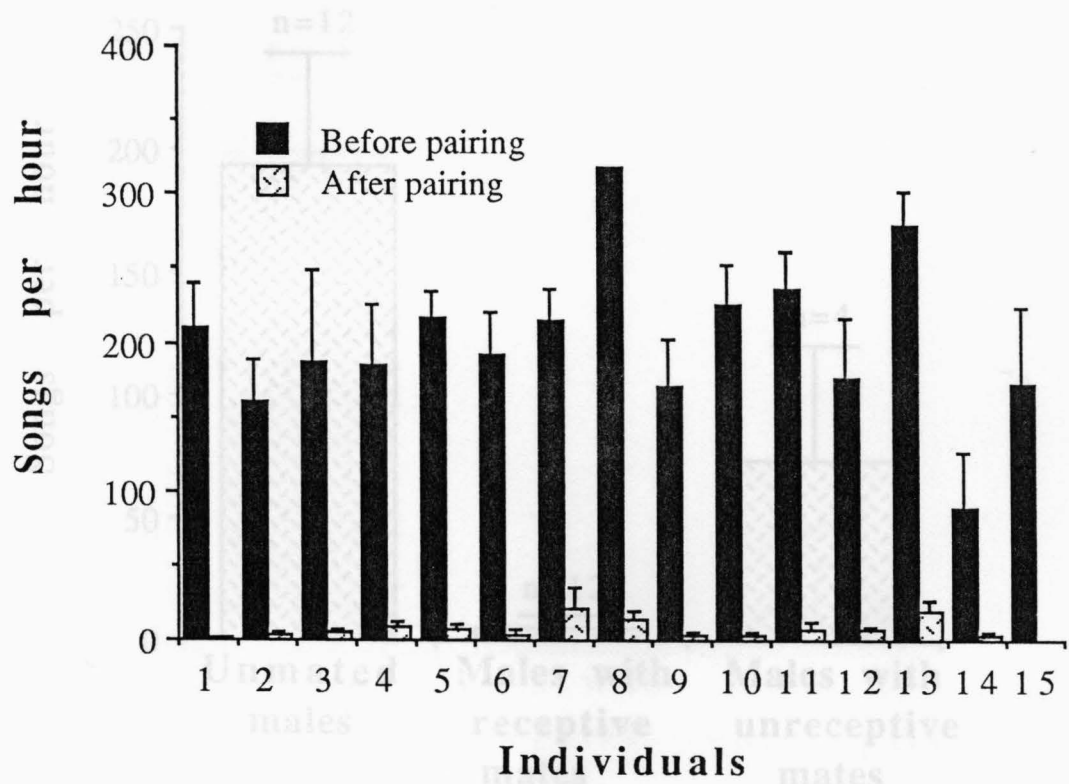


Figure 11. Song production by males before and after pairing- 1990

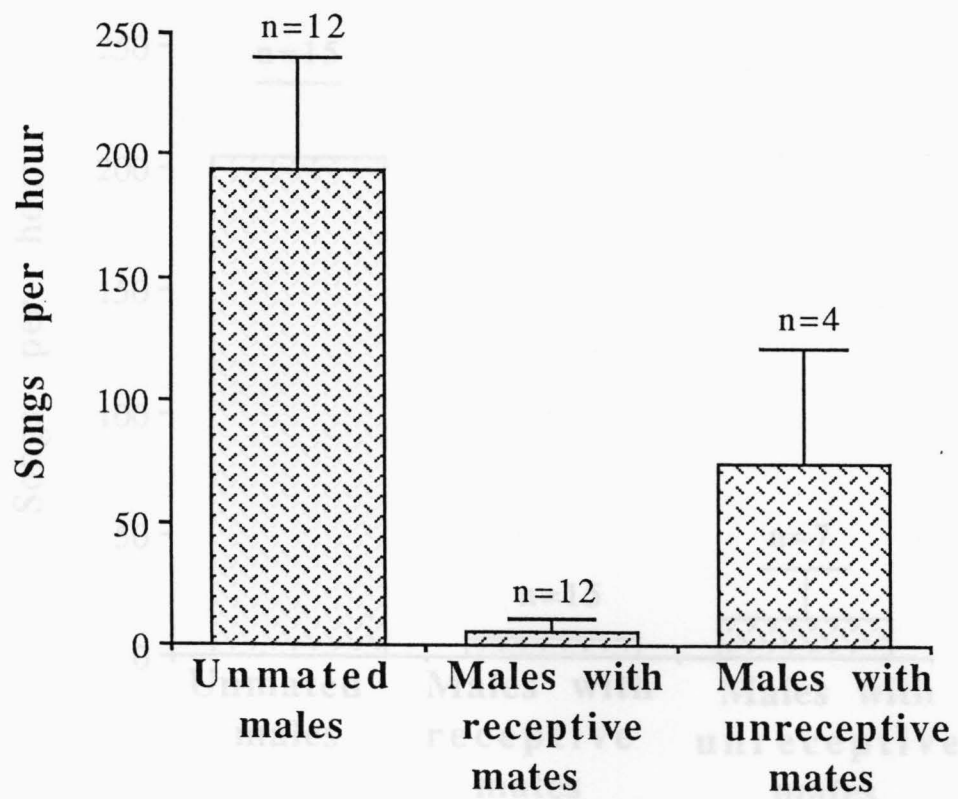
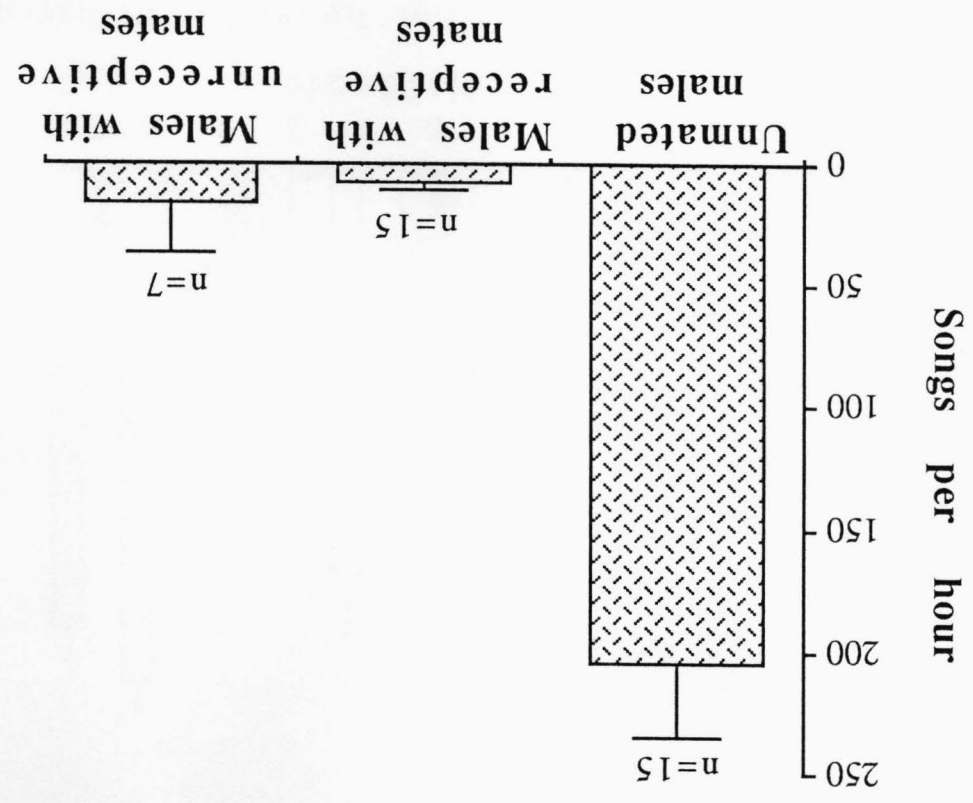


Figure 12. Seasonal song rates- 1989

Figure 13. Seasonal song rates- 1990



Males before desertion vs. Males after desertion

After pairing, males almost ceased singing until their young fledged or, more commonly, until they were abandoned by their mates. Following desertion, males greatly increased song production ($P=.0005$ in 1989, $P=.0078$ in 1990; Figures 14 and 15).

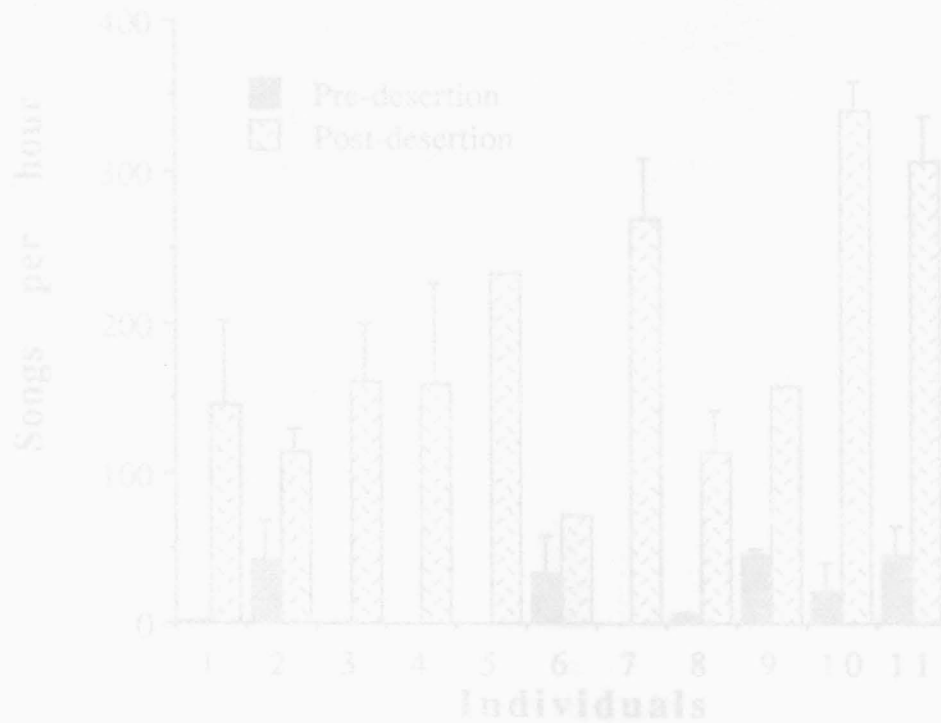


Figure 14. Song production by males before and after desertion by females- 1989

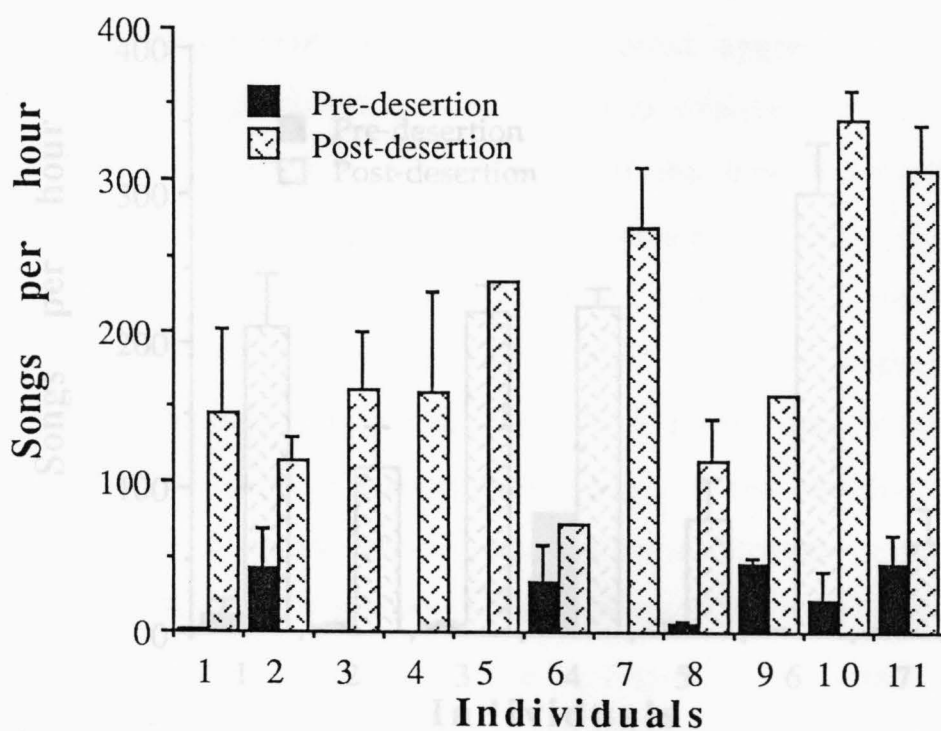


Figure 14. Song production by males before and after desertion by females- 1989

DISCUSSION

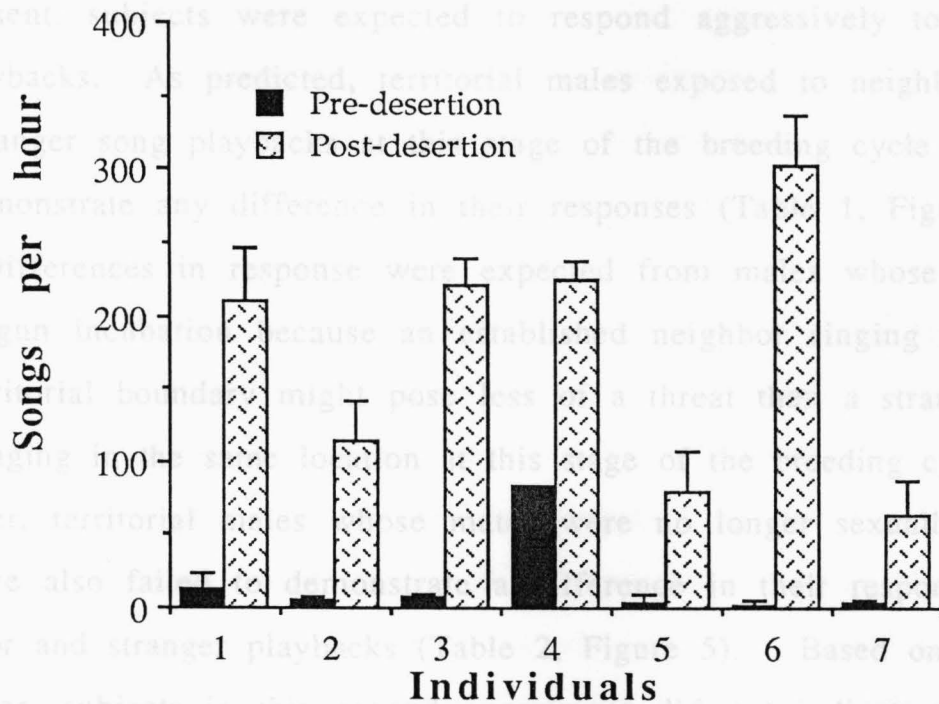
Lack of neighbor/stranger discrimination was predicted while a male's mate was sexually receptive because all conspecific males posed a potential threat to the resident's paternity. In this

experiment, males were expected to respond aggressively toward all playbacks. As predicted, territorial males exposed to neighbor and stranger song playbacks during the breeding cycle did not demonstrate any difference in their responses (Table 1, Figure 4).

Differences in response were expected from males whose mates had begun to desert because an established neighbor singing along the territorial boundary might pose less of a threat to a strange bird singing alone. This change in the breeding cycle, however, territorial males whose mates were sexually receptive also failed to discriminate between neighbor and stranger song playbacks (Table 2, Figure 5). Based on their responses, subjects in this second experiment did not indicate that

simulated territorial encounters.

Figure 15. Song production by males before and after desertion by females- 1990



Evaluation of Experimental Procedures

The lack of difference in the response of resident males later in the breeding cycle could be attributed to certain aspects of experimental procedure. It is possible that not enough playbacks

DISCUSSION

Lack of neighbor/stranger discrimination was predicted while a male's mate was sexually receptive because all conspecific males posed a potential threat to the resident's paternity. In this experiment, subjects were expected to respond aggressively toward all playbacks. As predicted, territorial males exposed to neighbor and stranger song playbacks at this stage of the breeding cycle did not demonstrate any difference in their responses (Table 1, Figure 4).

Differences in response were expected from males whose mates had begun incubation because an established neighbor singing along the territorial boundary might pose less of a threat than a strange bird singing in the same location at this stage of the breeding cycle. However, territorial males whose mates were no longer sexually receptive also failed to demonstrate a difference in their response to neighbor and stranger playbacks (Table 2, Figure 5). Based on their responses, subjects in this second experiment did not indicate that there was a difference in the threat posed by these two types of simulated territorial encounters.

Evaluation of Experimental Procedures

The lack of difference in the response of resident males later in the breeding cycle could be attributed to certain aspects of experimental procedure. It is possible that not enough playbacks

were performed to sufficiently sample the response of males at this stage of the breeding cycle. Sample sizes for this experiment were low because few nesting attempts reached this stage because of high levels of nest destruction.

It is also possible that some of the variables used in these experiments were not appropriate measures of response. Catchpole (1977) writes:

If playback experiments are used as evidence in discussion of territorial behaviors...it is important to know how artificially elicited responses compare with natural aggressive encounters. (page 494)

Keller (1979) noted that male-male interactions in chipping sparrows involve chasing and a vertical flight in which the individuals grapple. This type of activity is generally initiated by a non-resident male's singing and is followed by the resident approaching the sound source. In artificial encounters, once the approach is made, the resident male continues flying over the vicinity of the speaker, presumably looking for the singer. Thus, the increase in flying activity, the nearness of approach, and the latency of response all correspond to behaviors observed in natural aggressive interactions and are appropriate measures of response. However, measuring response by the increase in singing activity might be the least precise method because male singing behavior in natural encounters is variable. In some cases, resident males sang in response to an intrusion, while in other cases the resident silently chased as the intruder continued to sing. Because singing activity increased in

some playbacks and decreased in others, an analysis was performed with this variable removed from the data. Even in this case, no significant difference exists.

One aspect of experimental procedure that varies among previous studies is the position of the playback speaker. Beecher and Stoddard (*personal communication*) performed playbacks to song sparrows, a species that previously had demonstrated only weak discrimination (Kroodsma 1976; Searcy *et al.* 1985). They used three speaker positions: along the appropriate boundary (*i.e.*, the boundary between the focal male and the individual whose song was used in the playback), in the territory center, and along an inappropriate boundary (*i.e.*, a boundary between the focal male and a neighbor other than the neighbor whose song was used in the playback). They found significant differences in response only when the speaker was placed along the appropriate boundary. They proposed that speaker positions elicited different levels of discrimination because the difference in threat value of the neighbor playback relative to the stranger playback was greatest along the appropriate boundary and decreased at the other locations. In my experiments, the speaker was positioned along the appropriate boundary in order to simulate the greatest relative difference in threat value for the two playbacks. Even under these circumstances, the subjects did not differ in their response to playbacks.

Of all the elements of this experiment that could affect the outcome, choice of study species is the most important. Individual recognition by song requires that listeners discriminate among

similar sounds of different individuals in the absence of other identifying cues. A good signal for individual recognition would be highly stereotyped within an individual, but vary among individuals. The songs of chipping sparrows have features that make each individual's song unique and recognizable to the human ear (Table 7) (Appendix I). An analysis by Marler and Isaac (1960) described the song as a repetition of identical syllables at constant intervals, with one syllable type being found in an individual. However, syllable structure varies among individuals, and this accounts for the ease of recognition by humans. The ability of birds to perceive differences in frequency (pitch) may not be as good as that found in humans, but, because birds are capable of temporal discrimination equal to or better than humans, it seems likely that the birds could detect this inter-individual variation (Greenewalt 1968; Dooling 1982).

Individual variation is necessary for individual recognition, and, upon close inspection, it likely exists in all species (Falls 1982). It is also likely that successive vocalizations produced by an individual might vary in minor ways. While individual variation, at least at some fine level, is probably universal, individual recognition occurs only when the variation within an individual is less than the variation among individuals.

In one of the first sonographic analyses of song, Marler and Isaac (1960) described the variation among the songs of eight male chipping sparrows and among the songs of one individual. Among individuals, there was variation in song duration, number of syllables

per second, syllable duration, interval between syllables, and frequency and amplitude characteristics of syllables. They detailed variation in these same features within the songs of one individual. If song is to be used for individual recognition, it will be based on those features that are relatively constant within an individual. In their analysis, the features most constant within an individual--number of syllables per second and frequency and amplitude characteristics of the syllables--were also shared by some members of the sample population. Whether this similarity was due to genetic factors, learning, or chance is not known. In any case, they wrote:

It is difficult to see how reliable individual recognition would be possible in this species. (page 133)

I performed a similar analysis with song of males in my study population. I also found that the features most constant within individuals--syllable length and syllable interval--were shared between two or more individuals (Table 7). However, the potential for discrimination does exist in the combination of features in each individual's song (Table 7, Appendix I). Although this potential exists, males in this population did not demonstrate discrimination in their response to playbacks of different individuals. Whether or not the birds are able to perceive these individual differences is not known, but the individual variation does not lead to different responses.

from neighbors (Walskrug 1964 and 1979; Evans 1964; Keller 1979). The frequency of interactions used to delineate territorial boundaries (see methods) varied with reproductive stage, and these behaviors were observed most frequently early in the

What Are Not the Functions of Chipping Sparrow Song

Territorial Defense

Since territorial defense is one of the most widely accepted functions of song, why song does not function in this manner in chipping sparrows needs to be addressed. The function of song is generally related to mating and spacing behavior in a species (Catchpole 1982), and male chipping sparrows might defend nest sites alone rather than nest sites and food resources.

Keller (1979) noted considerable variation in size, use, and defense of chipping sparrow territories. In the first year of her study, territory sizes ranged from 0.20-0.32 ha, with a mean of 0.24 ha, and, in the second year, they ranged from 0.36-0.93 ha, with a mean of 0.54 ha. These differences among individuals did not correspond to differences in reproductive success, which was determined largely by the incidence of nest predation. Larger territories could reduce predation by increasing nest spacing, but, because no interspecific territoriality was observed in her study or mine, size of chipping sparrow territories probably had little effect on dispersion of passerine nests in general.

Keller (1979) documented that males were observed within their territories 94% of the time. It has also been observed that males and family groups cross territorial boundaries without eliciting responses from neighbors (Walkinshaw 1944 and 1959; Evans 1964; Keller 1979). The frequency of interactions used to delineate territorial boundaries (see methods) varied with reproductive stage, and these behaviors were observed most frequently early in the

breeding cycle. Keller determined that the frequency of male-male chases was significantly different from that predicted if this behavior were independent of reproductive stage ($\chi^2 = 55.787$, $df = 5$, $P < 0.005$). This period of greatest territorial defense also coincides with the lowest levels of song output by a territorial male. Space may be defended by a male during this stage of the reproductive cycle to act as a buffer to guard a sexually receptive mate from extra-pair copulations (Møller 1990). Males seem to maintain this space exclusively by overt aggression without the help of song. After his mate has begun incubation, a male may intrude upon neighboring conspecifics at an earlier stage of reproduction and elicit territorial behaviors from them, but he demonstrates little in the way of defense of his own territory. Keller (1979) observed the boundaries of chipping sparrow territories to be plastic. The decrease or even cessation of territorial defense by a male after his own mate has begun incubation, combined with high levels of aggression still maintained by neighboring males at an earlier reproductive stage, could result in the shifting configuration and size of territories. Even in this type of territorial system song could be used for territorial defense, but, since chipping sparrow song output drops after pairing rather than after the onset of incubation, it seems unlikely that this species' song has a territorial defense function.

The lack of territorial function could also be related to the habitat. Like sedge warblers (*Acrocephalus schoenobanus*), another species in which song does not seem to be a major component of territory defense (Catchpole 1973), chipping sparrows live in fairly

open habitat that allows for visual communication. Because chipping sparrows breed at relatively high densities (Figure 3), a single male can be exposed to songs of up to seven conspecifics at a time; encoding territorial defense into visual displays could have a selective advantage because it reduces ambiguity. Some species have reduced ambiguity by having different songs for different functions (Lein 1972; Kroodsma 1981), but the combination of proximity and visibility available to chipping sparrows may have placed a premium on visual displays in this species. Males do seem to use the brightly colored chestnut crown in displays; these feathers are noticeably raised during male-male chases.

Territorial Establishment

While neighbor/stranger discrimination by song can be an important part of long-term territorial defense, it may not be a necessary feature in territorial establishment. Both in species where territories contain nest sites and food resources, and in species where territories are only nest sites, males establish exclusive areas to attract mates, and high rates of singing could be part of this process. Males may also need to re-establish territories following desertion by their mates. Song rates are indeed highest in male chipping sparrows during territorial establishment early in the breeding season and also following female desertions. However, these periods of increased song production also coincide with the times when males are without mates. Some males went several weeks without attracting mates and their song production never decreased. If song

does not function in territory defense but is an important part of territorial establishment, singing rates should decrease after a territory is obtained. Furthermore, territorial configurations and boundaries were frequently observed to shift without the owners of these territories increasing song production; song production increased only when shifts were made by unmated males.

There was also one case of a pair of unbanded birds moving from outside the study area into an area on the periphery of the territories of two banded males. This new male and his mate were in the process of building a nest the first day they were observed. No period of high song output was observed from this male before nest building began. A territory was established without the male producing high levels of song.

What Are the Functions of Chipping Sparrow Song

As stated earlier, there is a correlation between seasonal breeding activities and song output in most species. In a study of 20 woodland passerines, it was observed that song output maxima were reached several days prior to egg laying (Slagsvold 1977). In most of these cases it would be inappropriate to conclude that song has solely a sexual function because, while song output may decrease shortly after pairing, song is commonly produced persistently throughout the rest of the season. However, virtual song cessation after pairing would be strong evidence in favor of song having only a sexual function (Catchpole 1982). Effective song cessation has been established in the brown towhee (*Pipilo fuscus*), (Quaintance 1938;

Marshall 1964), and in the sedge warbler (Catchpole 1973). In both cases, the authors conclude that female attraction is the predominant function of these species' songs. Based on their pattern of singing in relation to their reproductive activity (Figures 10-13), chipping sparrows can be added to this list.

Even stronger support for the mate-attraction hypothesis comes from male behavior after loss of his mate. Krebs *et al.* (1981) demonstrated that even in great tits (*P. major*), a species in which song is thought to function predominantly in territorial defense, males increase song almost six-fold following female removal. Johnson (1983), describing the effects of natural mate loss on the singing behavior in plain titmice (*P. inornatus*), observed a nine-fold increase in singing activity. I observed increases of almost ten-fold in song production by male chipping sparrows following natural loss of their mates (Figures 14 and 15).

While evidence suggests that persistent song may have only a sexual function, the possibility that it may have an effect on neighboring males must be evaluated. Territorial and sexual functions can only be separated in the days immediately following pairing, because, at this point, the male is no longer attempting to attract additional females, but his efforts to guard his sexually receptive mate from conspecifics should be great. At this stage of the breeding cycle, song is virtually lacking in male chipping sparrows (Figures 12 and 13).

Some males increased song output while they were still paired, but this occurred only after incubation had begun, and this behavior

was quite variable. Increases in song output at this stage of reproduction are associated with males' attempts to become polygynous. Keller (1979) observed this in both years of her study, but I observed it only in the first year of mine. Changes in the relative numbers of males and females could have influenced male singing behavior in the different years of my study. I assessed the abundance of females by how long males went without mates and, in both 1989 and 1990, some males had difficulty attracting mates; I can not assume that there was a difference in the number of females over the two years. However, in 1990, there were more males breeding in the same area as in 1989. The potential increase in the number of males relative to the number of females could affect male reproductive strategies (Emlen and Oring, 1977). As the number of males increased and the potential for polygyny decreased in 1990, males did not demonstrate increased song production after their mates began incubation. Male chipping sparrows appear to be opportunistic because song production increased only when the potential for polygyny existed.

Relationship of Song Structure and Function in Chipping Sparrows

Much ornithological work has concentrated on determining the functional significance of physical features of song. Marler and Isaac (1960) proposed that advertising song is subject to conflicting pressures because of its dual function. Intrasexual selection would favor features that increase success in male-male contests, while

intersexual selection would favor features that increase song's attractiveness to females. Based on observations of song complexity and singing behavior among species of *Acrocephalus*, Catchpole (1980) proposed a mechanism for the evolution of song features related to their functions. He argues that song used for territorial defense will be short, simple, and stereotyped, while song used primarily in mate attraction will be long, complex, and variable (Figure 16).

This argument relies largely upon the relationship between mating system and the strength of sexual selection, and it assumes that more intense sexual selection pressure is found in polygynous mating systems. Kroodsma (1977) noted that song complexity increased in the North American wrens as the occurrence of polygyny increased. Catchpole (1980) observed the opposite pattern in *Acrocephalus*, with complex songs being found in the monogamous species. Catchpole's observations appear to run contrary to the idea that increased sexual selection in polygynous mating systems leads to increased song complexity, but this is where the distinction between direct and indirect female choice is important (Figure 16). In monogamous species of *Acrocephalus*, territories are small, food resources are found outside the territories, and both sexes feed young equally. Female choice in these species could be based directly on male quality, and song could be used by females as an indicator of male quality. In the polygynous species, territories are large and rich in food resources and males provide little parental care. Females could use features associated with territory quality as

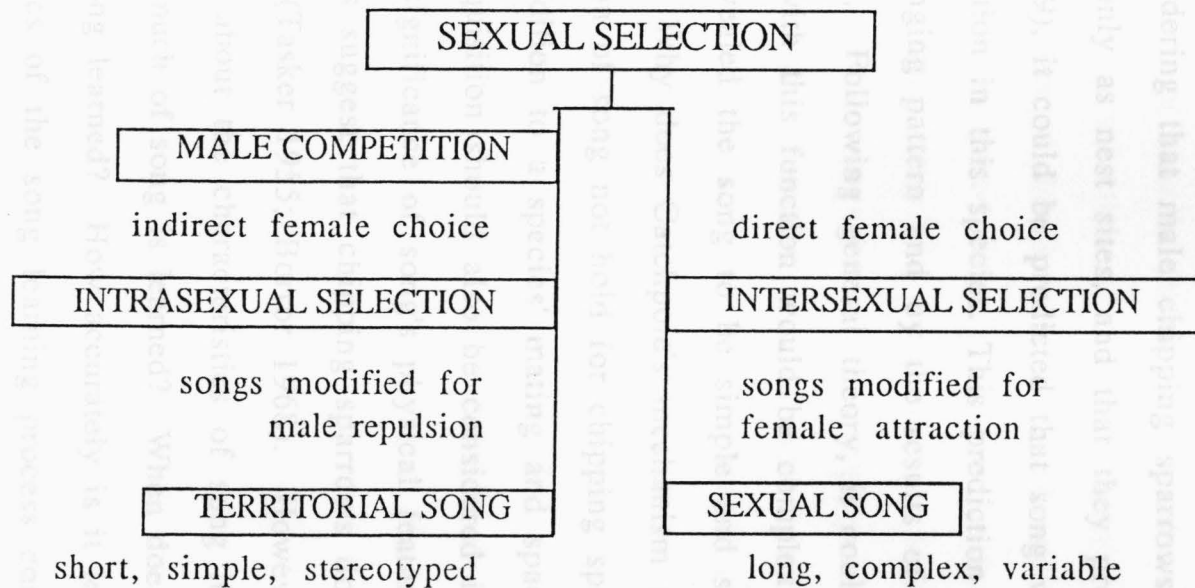


Figure 16. Sexual selection and the evolution of two main types of song in passerine birds (Catchpole 1982) (copyright by Academic Press, Inc. 1982)

cues for mate choice (indirect choice of males). In these species, short, simple, stereotyped songs may have developed by intrasexual selection pressure to be effective in territory defense (Catchpole 1980).

Considering that male chipping sparrows might defend territories only as nest sites, and that they provide parental care (Keller 1979), it could be predicted that song would have solely a sexual function in this species. This prediction is supported by the seasonal singing pattern and by the results of the playback experiments. Following general theory, it could also be predicted that song with this function would be complex and variable, but my analysis revealed the song to be simple and stereotyped within an individual. Why does Catchpole's mechanism for sexual selection and the evolution of song not hold for chipping sparrows (Figure 16)?

In addition to a species' mating and spacing system, the pattern of song acquisition should also be considered in discussing the functional significance of song's physical features. Previous observations suggest that chipping sparrows do have the ability to learn song (Tasker 1955; Borror 1968). However, there is no information about the characteristics of song learning in this species (*e.g.* How much of song is learned? When does learning occur? From whom is song learned? How accurately is it learned?). These characteristics of the song learning process contribute to the physical features of song by resulting in song sharing among kin, song sharing between neighbors, or song variation over time and space. Some of these consequences may confer a selective advantage in interactions

with neighbors (Payne 1983; Payne 1985), in matching song features to habitat (Wasserman 1979; Gish and Morton 1981; Anderson and Conner 1985), or in leading to assortative matings (Nottebohm and Sclander 1972; McGregor and Krebs 1982). Some of these consequences may also be mere by-products of the song learning process, with no selective advantage (Slater 1989).

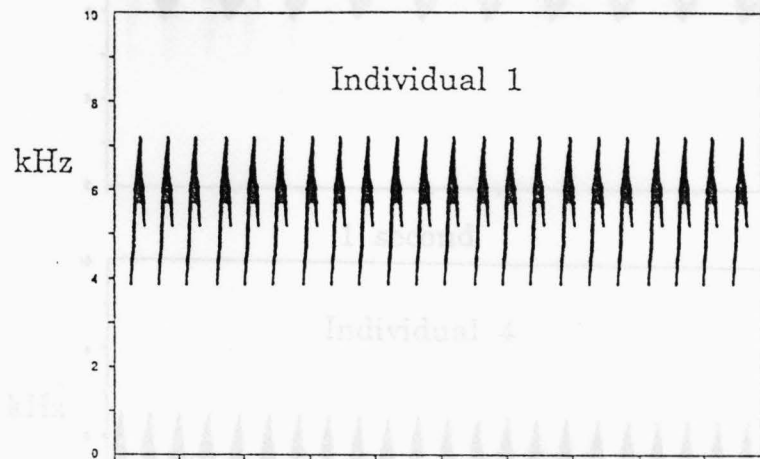
Discussions of the functional significance of the consequences of song learning are based largely on information gathered from species with dual function song. In these species, song is subject to conflicting selective pressures. In chipping sparrows, song has solely a sexual function. The development and function of song will be related, but how the absence of a territorial function affects the song learning process and how this contributes to the physical features of song is not known. There needs to be an understanding of which features of chipping sparrow song confer a selective advantage and which features of song are by-products of the learning process before the functional significance of the physical features of chipping sparrow song can be evaluated.

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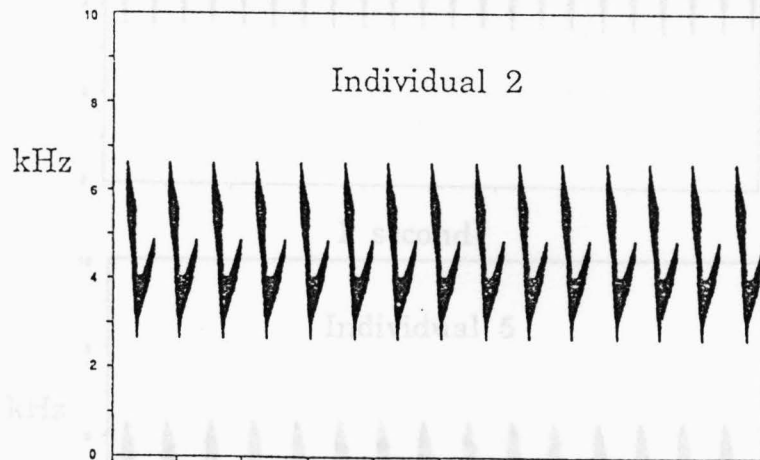
Typical sound spectrographs of individuals used in playback experiments.

Appendix I

Typical sound spectrographs of individuals used in playback experiments.

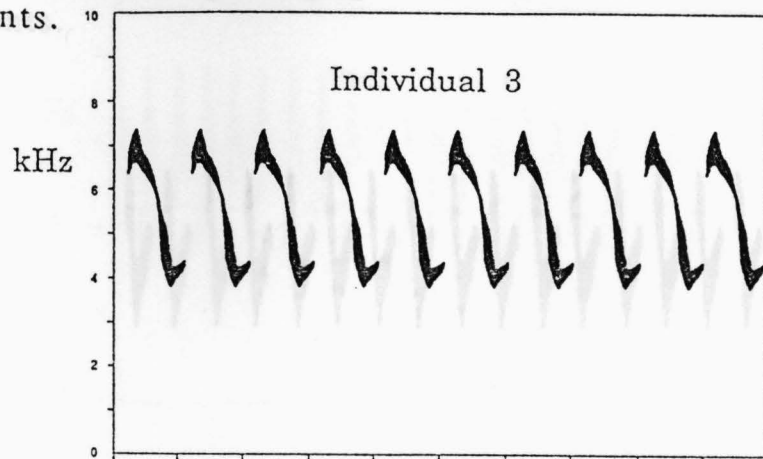


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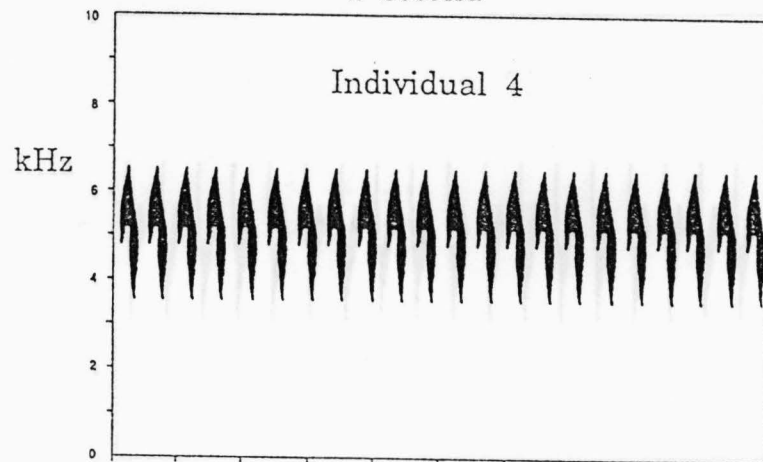


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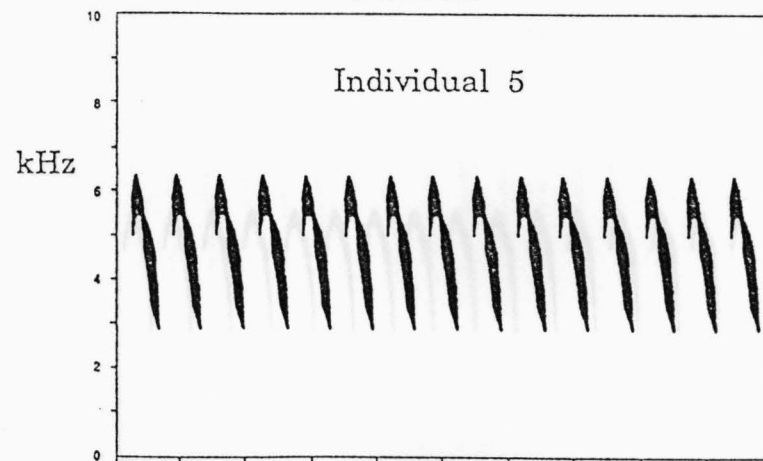
Typical sound spectrographs of individuals used in playback experiments.



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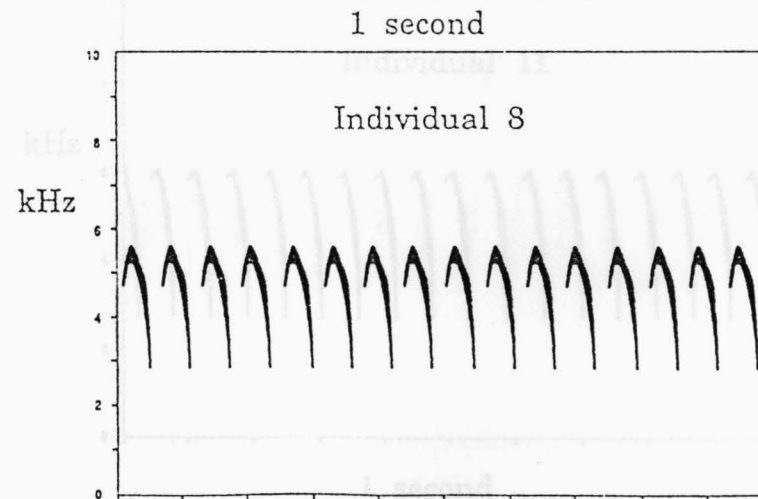
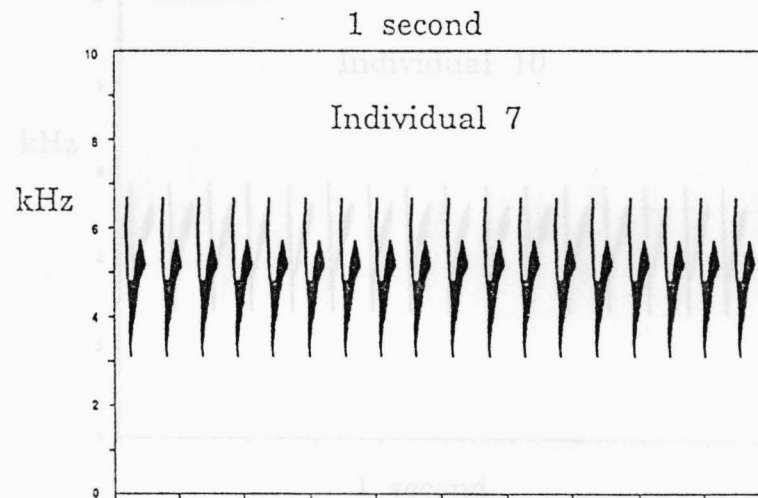
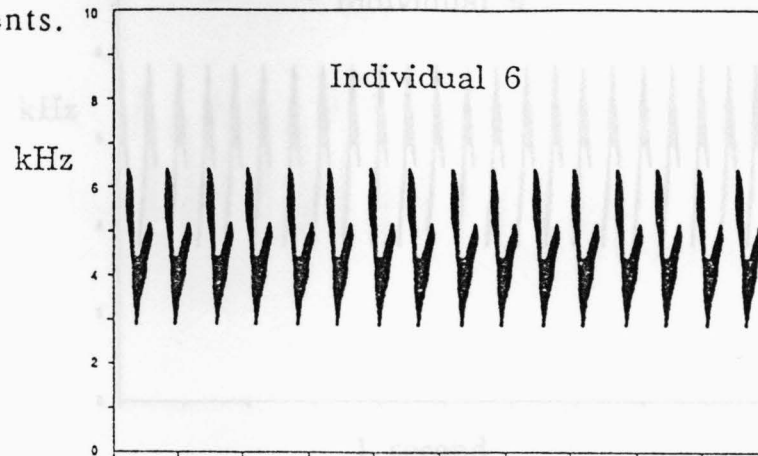


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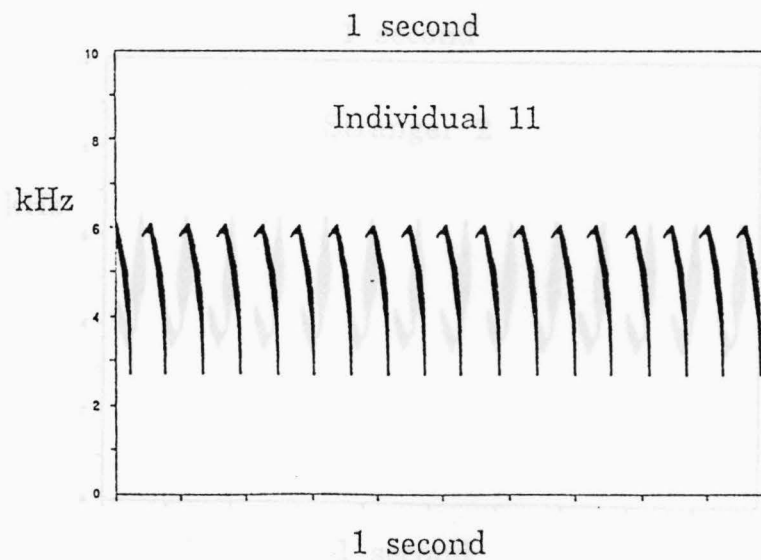
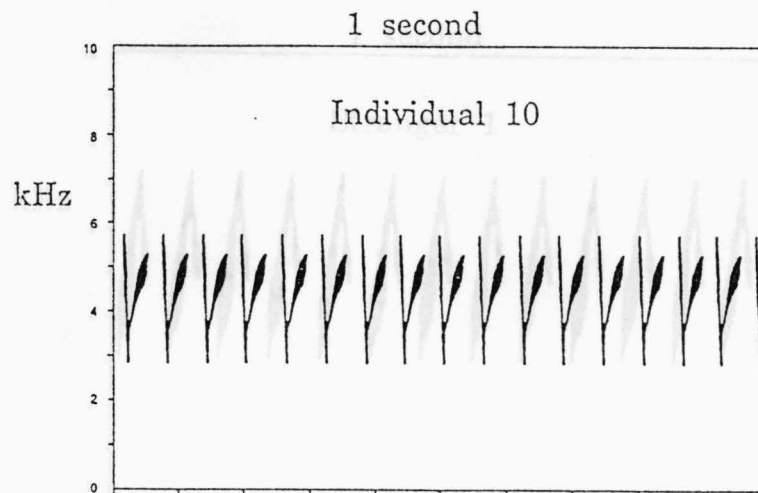
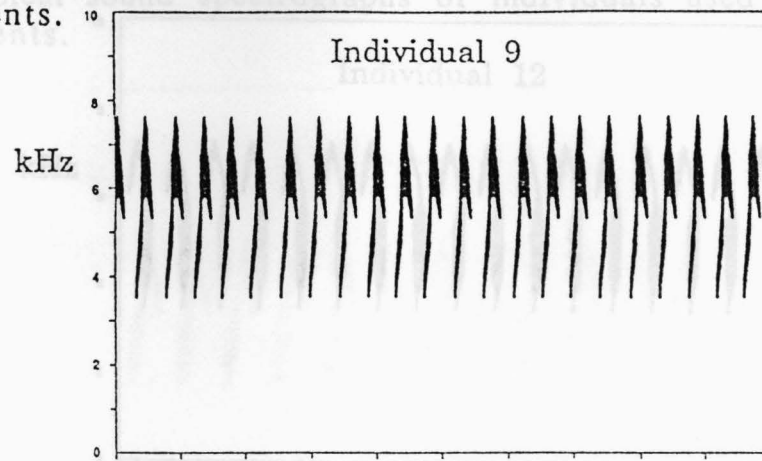
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Typical sound spectrographs of individuals used in playback experiments.

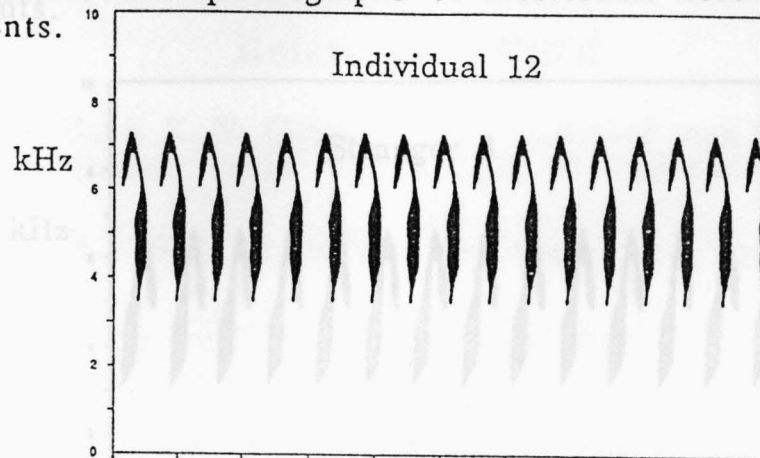


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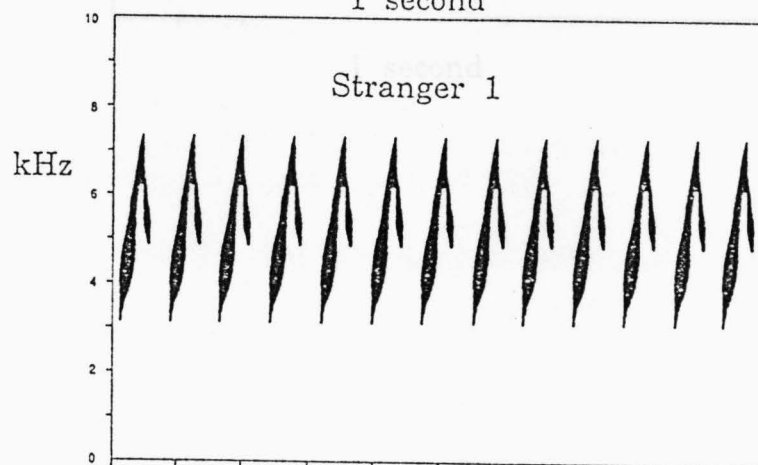
Typical sound spectrographs of individuals used in playback experiments.



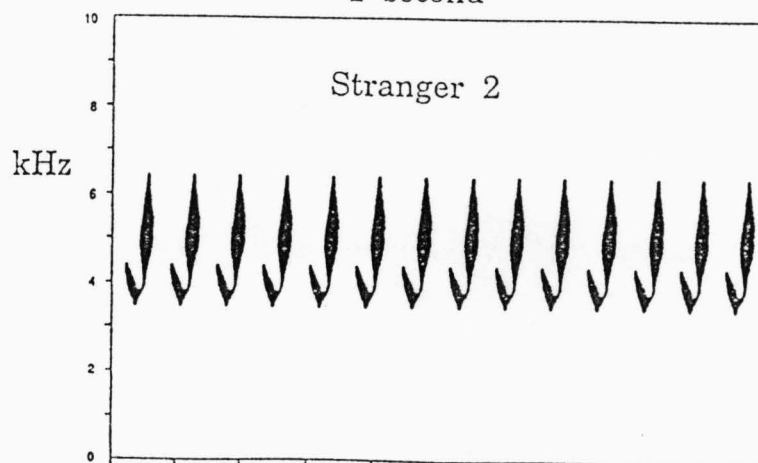
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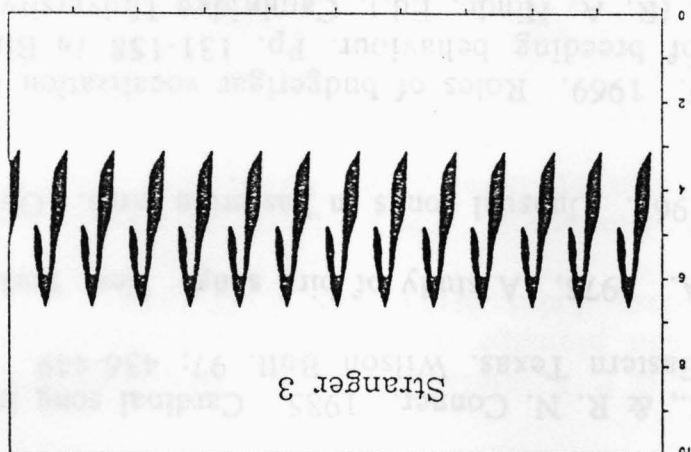


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Typical sound spectrographs of individuals used in playback experiments.



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